VII. THE DAVID FERRIER LECTURE.—*On Some Correlations Between Skull and Brain.*

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[PLATES 36–48.]

MR. PRESIDENT AND GENTLEMEN,

My most pleasant duty to-day is to thank your Council for the honour that it has conferred upon me by inviting me to give the second lecture in memory of the late Sir DAVID FERRIER.

I have accepted this invitation with feelings of gratitude, not only to your Council, but also for the contributions made in this country to our knowledge of the structure and function of the nervous system. Among these, the works of Sir DAVID FERRIER, however prominent, only stand out as a conspicuous example of a national tradition, maintained in recent years, both in the Physiology and Anatomy of the brain.

The task I have accepted is not an easy one, the less so as the first Ferrier lecture was given by Sir CHARLES SHERRINGTON who, in both the methods and results of his investigations, attained a degree of exactness at which morphologists aim in vain.

As, however, your Council, considering FERRIER's physiological as well as anatomical merits, thought it appropriate that the second lecture should be a morphological one, I hoped that a subject related to the anthropology of the brain might be acceptable.

Anybody dealing with this subject knows how many difficulties are encountered in this field, and how anatomists were misled into taking individual variations for racial characters and making physiological or even psychological deductions from the error.

While such mistakes can only be overcome by a sufficient *quantity* of material—which is not so easy to obtain—another stumbling block in this field of investigation is the *quality* of the material, which, collected in foreign continents, is rarely preserved as it should be for such purposes. But even if this is well done, the mere position in which the material is held during transport may render it practically worthless.

Furthermore, exact data concerning the skulls from which the material is taken are desirable here, as one of the first points to be examined is the correlation between brain and skull form, in order to find out which of the morphological features of the brain are

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correlated with, and perhaps primarily depend upon, the racial or other characteristics of the skull, and which may depend on the brain itself.

Considering the material and scientific difficulties involved, you will not expect from me a solution of the problems connected with this subject. I shall be content if I succeed only in establishing certain rules that should be considered in this matter, especially concerning some correlations between the brain and mechanical influences acting on it.

Although it has long been recognised that the correlation between skull and brain form is a mutual one, the influence of enlargement of the brain on the skull, in individual and phylogenetic development, has impressed us more than anything else; and the conviction prevails among anatomists (SCHWALBE, 1907) that usually the characteristics of the brain are primary to those of the brain case.

For anthropology this question involves an important point, since if the morphological encephalic differences in various races are primary, these differences might point to great intrinsic cerebral varieties amongst man, whereas if the brain case is largely responsible for the various forms of its contents, the racial differences in the brain, though remaining equally conspicuous, would not necessarily imply intrinsic cerebral varieties. It is evident that the same holds good for animals.

It is for this reason that I shall begin by discussing some examples in which the opposite is true, *i.e.*, in which the envelope seems to be responsible for the form of its contents. Such examples occur not only among mammals; they are even more evident in lower vertebrates, especially in fishes and birds.

Thus in Teleostomes the influence of external pressure on the brain is very evident, and is the more striking because this influence is only exercised in a larval stage, though its effect lasts throughout life.

It is well known that the forebrain of Teleostomes is fundamentally different from that in practically all other vertebrates.

Whereas in Cyclostomes, Plagiostomes and all vertebrates higher than fishes, the upper part of the forebrain forms a real mantle, covering the ventricles like a roof; in Teleostomes the dorsal part of the telencephalic tube, which contains the primordium of the pallium, does not grow out in a mantle-like extension, but only increases in thickness, forming a solid mass. This grows into the ventricle close to the striatum and therefore is rightly called "epistriatum."

This epistriatum and the ventricle itself are only covered by a choroid membrane, which extends in width as the transverse increase of the epistriatum pushes its lateral insertions further apart.

The same increase causes the dorso-lateral wall of the forebrain to turn down, so that the originally dorsal edge of the telencephalic tube, instead of growing out in a dorso-medial direction, is pushed ventro-laterally, so far, even, that not uncommonly its originally dorsal edge becomes the most ventral part of the forebrain.

The reason for this curious growth is, I believe, to be sought for in the dorso-ventral compression, the flattened condition of the Teleostome head in its larval stages.*

The flattening of the head—already mentioned by BALFOUR and PARKER (1882) and by BASHFORD DEAN (1895, 1896), for *Lepidosteus* and by the latter also for *Amia*, according to Dr. DE BEER, who is such an expert on the development of the relations in Teleostomi—is associated with the following relations. (Personal communication.)

(1) The anterior headfold in the embryo is not so pronounced in Teleostomi as in Selachii and Amniota, and as there is a large quantity of yolk present in the egg, this results in the head being as it were plastered down and expanded laterally instead of dorsally. Perhaps also the tough resistant chorion differs from that of other vertebrates, and it is significant that it is only in the Teleostomi that the Müllerian duct is replaced by a special oviduct.

(2) A certain amount of space within the cranial cavity is occupied by the recti oculi muscles, pressing back dorsally the trabeculae cranii to enter their myodome: again confined to Teleostomi.

It is certainly true that in Teleostei the floor of the brain is lifted some way up off the floor of the cranial cavity and crammed up sideways against the auditory capsules (the median walls of which are here membranous) and the roof.

(3) The roof of the neurocranium is incapable of indefinite extension and stretching upwards as in the Amniota because it is still largely cartilaginous. In the Amniota the roof of the neurocranium remains membranous and only a tiny tectum synoticum is formed in cartilage.†

So in Teleostomes a dorso-ventral compression seems to prevent the pallial primordium from developing normally and causes the dorsal part to find a way by expanding transversely into the ventricle, as well as sideways. The epistriatum in some cases fills out the ventricle so far as to touch and coalesce with the septum, *e.g.*, in the Synbranchidæ (VAN DER HORST, 1917). The influence of compression is also seen in other parts of the central nervous system in these animals; thus the cerebellum is much more compact than in other fishes, and its ventricle, so conspicuous in Plagiostomes, is almost entirely obliterated (*V.* FRANZ, 1911), while the fourth ventricle also is very narrow.

This solid character of the central nervous system remains in the adult, when the skull has usually grown considerably, especially in the larger species, but also in some smaller ones (*e.g.*, *Girardinus*); the pericerebral space being filled up by a loose perimeningial tissue.

Mechanical factors acting during the larval stages may thus give the Teleostome forebrain its peculiar form. This for several years has puzzled comparative neurologists,

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* I must add though that a considerable pressure on the central nervous system also occurs in Cyclostomes as has been recently described by LE ROY CONEL (1929) for *Bdellostoma Stouti*. This author pointed out that the yolk in this animal's egg is very dense and contained in a tough shell immediately under which the central nervous system develops. Moreover, as the embryo grows in length the head is forced through the dense yolk in front of it, thus causing an antero-posterior pressure. As a result the whole nervous system shows a considerable compression, which only partly disappears after hatching. It must, however, be added that the forebrain in these animals, though obliterated, is not everted.

† It is true that the neurocranium is cartilaginously roofed in Selachii, where the brain is not flattened, but in these fishes the conditions (1) and (2) mentioned above do not apply. It is also true that a cartilaginous roof is present in Amphibia, but their embryos seem to be blown out with lymph and loose mesenchyme (DE BEER; personal communication).

since formerly the only criterion for pallial derivatives was a cortex-like, laminated arrangement of cells which we now know may fail even in a normally developed (inverted) mantle* as observed in birds. In the latter, a large part of what *consensu omnium* is called mantle is provided with cells that show no cortical lamination whatever, although in other parts lamination may occur (CRAIGIE,† 1929).

Also in birds a subpallial ventricular outgrowth seems to allow for pallial extension.

The telencephalon of the chick embryo of the 5th day of incubation still shows very wide ventricles roofed by the mantle. This condition changes during further development (ARIËNS KAPPERS, 1922). The mantle, instead of increasing in extent as does the mammalian cortex, shows—beginning fronto-laterally—a ventricular thickening which covers the real striatum with a hyperstriatal layer as it was called by EDINGER, WALLENBERG and HOLMES (1903), which, increasing, soon fills up nearly the whole ventricle.

Although this ventricular growth of the mantle may be favoured by the neurobiotactic influence of the numerous fibres ascending to it from the thalamus and other fibres connecting it with the underlying striatum—as ELLIOT SMITH (1919) stated—this factor probably is not the only one.

Mechanical factors may play a part. The first, a local one, is the fronto-lateral pressure of the large eyes on the brain. This not only prevents a free extension of the forebrain in frontal direction but it also lifts up the brain, thus influencing the angle of the brain-axis to the foramen magnum (cf. KÜENZI, 1918). The other factor, a general one, is the large quantity of the brain, together with the fact that the chondrocranium ossifies in a very early embryonic period and that the skull, especially the neurocranium synostoses early, the sutures having disappeared in nearly all birds in a few months (KRUMBACH, 1927). While the adult brain weight (of the chick) is acquired after 5 months, the brain increase between the 2nd and 5th months is still about half the brain weight of the 2 months chicken (LATIMER, 1925). Besides, the *indice de valeur cérébrale*‡ in the newborn chicken is only 0·68 of the adult.

So, whereas in Teleosts only a dorso-ventral compression in the larval stages causes the intraventricular growth, in birds the influence of the brain case or of the head as a whole may be responsible for it. Also, this influence does not assert itself in the earlier stages but somewhat later, when the brain mass increases far more than the skull, which is the opposite of what occurs in Teleostomes. To realize the exceptional quantity of the avian brain we should consider that the relative brainweight in birds, compared with the reptilia, is excessively high. This is best expressed by the cephalisation coefficient of DUBOIS.

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* Besides a laminated arrangement of cells may occur also in non-pallial parts, *e.g.*, at the bottom of the forebrain, so with the nucleus basalis of sharks.

† The cerebral cortex of Apteryx. Evidence that the avian neocortex has been reduced from a multilaminar condition. See also 'Jn. of Comp. Neur.,' Vol. 49, 1930.

‡ Calculated from LATIMER's body and brainweight figures, according to DUBOIS' formula $K = \frac{E}{P^r}$, in which $r = 0{\cdot}25$ (for further details of this *indice de valeur cérébrale, see* p. 399).

The adjoining table gives the cephalisation coefficient (K) of some avian brains compared to that of some reptiles and mammals, calculated with DUBOIS' formula $K = \frac{E}{P^r}$, in which $r = 0 \cdot 56$.

Reptiles and birds.	Cephal. coeff.	Author.	Mammals.	Cephal. coeff.	Author.
Testudo græca	0·0075	DUBOIS (1913)	*Vespertilio mur. et myst.*	0·043	DUBOIS (1897)
Naja melanoleuca	0·0098	,,			
Vipera berus	0·010	,,	*Didelphys marsup.*	0·067	,,
Lacerta vivipara	0·012	FREDERIKSE (1931)	*Sorex vulgaris*	0·069	,,
			Talpa europea	0·075	,,
Varanus niloticus	0·016	DUBOIS (1913)	*Mus decumanus*	0·077	,,
Lacerta agilis	0·018	,,	*Mus musculus*	0·078	,,
Gecko gecko	0·018	,,	*Erinaceous europ.*	0·081	,,
Crocodilus porosus	0·019	Institute*	*Lepus caniculus*	0·172	,,
Gallus domesticus	0·045	,,	*Tupaja javanica*	0·187	,,
Phasianus colchicus	0·06	LAPICQUE and GIRARD (1905)	*Pteropus edulis*	0·193	,,
Pavo cristatus	0·07		*Tapirus americ.*	0·202	,,
Columba domestica	0·08	,,	*Sciurus bicolor.*	0·206	,,
Anas boschas	0·12	,,	*Sciurus vulgaris*	0·211	,,
Larus argentatus	0·13	,,	*Mustela putorious*	0·216	,,
Dendrocygna spec.	0·14	,,	*Tragulus javanic.*	0·220	,,
Buteo vulgaris	0·15	,,	*Paradoxurus mus.*	0·241	,,
Pica rustica	0·24	,,	*Viverra civetta*	0·262	,,
Garrulus glandarius	0·25	,,	*Canis fam. Leonb.*	0·283	,,
Corvus mondula	0·26	,,	*Canis fam. St. Bernh.*	0·285	,,
Corvus cornix	0·26	,,	*Felis leo*	0·309	,,
Paleornis docilis	0·29	,,	*Felis domestica*	0·328	,,
Chrysothrix amazon	0·30	,,			

*The brainweight of this crocodile was 13·9 gr., the length of the body 3·4 m., the bodyweight approximately 120 kg., rather more than less.

From this we see that the cephalisation in birds is much higher than in the most highly cephalised reptiles—including what perhaps is their nearest reptilian relative, the crocodile—and that in several birds it is higher than in many mammals, and in parrots it even comes near that of the Canidæ and Felidæ.

The high cephalisation of parrots explains the fact that while in adult humming birds (CRAIGIE, 1928) and various other birds (HUBER and CROSBY, 1929) there still remains both medially and laterally a small ventricular split, this small lateral split is entirely obliterated in parrots, the medial ventricular space has become extremely small, and nearly the whole forebrain has become one solid mass.

The size of the brain case being apparently limited, the nervous substance fills up all the space available. This also happens in the midbrain, the ventricle of which is equally reduced, while the *tecta optica* are pushed down by the caudal pole of the forebrain, thus making as much use as possible of the available endocranial space.

Anyone who has dissected an avian brain knows how closely the central nervous system in these animals lies against the neurocranium, a fact also demonstrated by

T. Edinger (1929), who showed that on an endocranial cast of a bird practically all the details of its external brain morphology may be observed, even the fine cerebellar fissures.

As this holds good for small as well as for large species it seems that space economy acts a part in this peculiar condition.

In mammals we meet with another way in which spacial relations work. To understand this we have to consider two rules concerning the gross anatomical correlations of brain and skull. The correlation is a double one.

The first one is that if two mammals of the same (or a related) genus differ in size (*ceteris paribus*) the brain of the tallest animal has the smallest length-breadth index.

The second correlation is that if two mammals of approximately the same genus and size differ in cephalisation coefficient, the brain with the largest cephalisation coefficient will have the greatest length-breadth index.

In the first case the correlation depends primarily on the body, in the second case primarily on the brain.

In order to illustrate the first case I give in Table I a series of mammals of the same genus but differing in body size. Opposite the name of the animal the length-breadth index of its brain is stated.*

TABLE I.

Order and species.	Br. ind.	Order and species.	Br. ind.	Order and species.	Br. ind.
Cervidæ :		Giraffidæ		Felidæ	
Cervulus muntjac	85·8	*Ocapia Johnstoni*	94·0	*Felis domest.*	93·0
Capreolus capræ	83·9	*Camelopardalis giraffa*	86·6	*Felis pardal.*	91·0
Rucervus duvauceli	77·5			*Felis concol.*	84·5
				Felis tigris	84·1
		Canidæ :			
Antilopes :		*Can. fam. Griffon*	90·2		
Gazella dorcas	90·1	*Can. fam. Spaniel*	81·0	Pinnipedia :	
Damaliscus albifrons	86·3	*Can. fam. German dog species*	74·0	*Phoca vitul.*	116·9
Taurotragus oryx	84·4			*Zalophus cal.*	100·0

As in each group the animals mentioned do not, or hardly, differ in brain organisation as expressed by its cephalisation coefficient, the differences in the general shape of the brain have to be explained by the differences in body size. As the cerebral organisation in the smaller species remains the same, but the length of the head decreases, the index of the skull increases, as has been pointed out by Klatt (1913)†.

Here the influence of body size is primary and the form of the brain its consequence.

In the second case, however, the difference in brain shape depends both on the skull and brain, but primarily on the brain. In animals of the same genus, or at least of the

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* For more figures *see* Ariëns Kappers (1927).

† Klatt, 'Ueber den Einfluss der Gesamtgrösse auf das Schädelbild. Arch. Ent.Mech.,' Vol. 36, 1913.

same order, but differing in cephalisation, the animal with the greatest cephalisation coefficient has a brain the size of which goes beyond the average size of its group.

In order to accommodate the larger brain the skull tends to become rounder and so the length-breadth and also the height-breadth indices increase.

To illustrate this I refer to Plate 36 showing the brains of a Malay and Ice bear and of a dog, and to the list of indices in Table II. From both it appears that in the lesser cephalised animals the brain is more elongated, while in the higher cephalised ones it is rounder.*

TABLE II.

Orders and species.	Br. ind.	Order and species.	Br. ind.	Order and species.	Br. ind.
		Carnivora			
Marsupials :		Viverridæ :		Prosimiæ :	
Metachirus opossum	70·4	*Paradoxurus mus.*	76·2	*Lemur mongoz* . . .	83·8
Macropus robustus .	92·0	*Arctitis bintur.* . .	78·0	*Cheiromys madag* . .	95·8
Rodents :		Canidæ :		Western monkeys :	
Cavia cobaya . .	93·7	*Canis fam. St. Ber.*	77·0	*Callithrix jacch.* . .	70·3
Dolichotis patagon. .	120·0			*Cebus apella* . . .	78·3
Ungulates :		Ursidæ :		Catarrhine monk :	
Sus scrofa dom. . .	78·0	*Nasua rufa* . . .	72·0	*Macacus nemestr.* . .	80·0
Capra hircus . .	83·0	*Procyon cancriv.* .	81·4	*Symphalang. synd.* .	80·0
Equus asinus . .	95·0	*Ursus malayan* . .	90·4	*Troglodytes Schw.* .	84·2

To understand these figures we have to realise that the cephalisation coefficient of *Macropus robustus* is about twice as large as that of the opossum. This explains that notwithstanding the greater size of the Macropodidæ their brain index is smaller, the brain tending to a rounder form on account of its greater quantity, to be kept within a limited space. The same holds good for *Dolichotis patagonica* whose cephalisation coefficient is about twice that of *Cavia* (*aperea*, the wild form of *cobaya*).

The Ungulates mentioned in my list did not differ very much in body weight, but the cephalisation coefficient in the goat is about one and a half times that of the donkey, and twice as large as that of the pig. Accordingly the goat's brain is more brachycephalic than that of the pig, while the donkey's brain even has an index of 95.

Of the Carnivores mentioned *Ursus malayanus* has the largest cephalisation coefficient ((0·75), about twice as large as in Viverridæ and dogs and one and a half times larger than in the *Nasuæ*). In harmony with this is the fact that notwithstanding the taller body size of *Ursus* its brain-index is larger than that of the other Carnivores mentioned in the table.

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* To make the comparison accurate the animals should not differ in body size. It is very difficult to find animals of exactly the same size and order differing exclusively in cephalisation coefficient. The list in Table II gives the best examples I could obtain. As body increase tends to diminish the brain index (*vide supra*) the influence of the cephalisation coefficient is still more evident in those of my cases, where —notwithstanding a taller body—the brain index is larger.

Similarly with the Prosimiæ and Monkeys. The cephalisation of *Cheiromys* is about twice as large as that of this *Lemur* and the coefficient of *Cebus apella* is no less than four times larger than that of *Callithrix*. Finally, the more cephalised Chimpanzee has a more brachycephalic brain than the Macaque and the Gibbon.*

Although these relationships are very simple they have not always been realised, neither have their consequences as regards the general character of fissuration been sufficiently emphasised. That their influence on fissuration is not only limited to a more arched or perpendicular course of fissures in the more cephalised species is best demonstrated by a comparison of the brain of the dog and bear† (Plate 36), keeping in mind that the cephalisation of the latter is about twice that of the dog and its brain index 90·4, while that of this dog was 77·0. The more sharply curved arcuate and corono-lateral fissures in the bear are at once evident. Another difference between the Ursine brain and that of dogs only comes to view if we open the Ursine pseudo-sylvian fissure. We then find that the two ecto-sylvian fissures, which in the dog lie on the surface, are entirely submerged and operculated in the bear. Even the anterior branch of supra-sylvian (see *Ursus maritimus*) tends to join the pseudo-sylvian fissure.

Other features are the steeper course of the presylvia and the tendency of various fissures to make transverse branches and *processus acuminis*.

Thus in mammals a correlation between the form of the brain and the expansion possibilities of the skull is evident.

Also examples of more localised compressions could be given, such as the formation of the cruciate sulcus in Carnivores by pressure of the frontal bones, but as the aim of my paper is only to trace some general lines, I shall not mention special cases.

Hitherto I have only spoken of adult animals, but comparing newborn and adult mammals of the same species we see both factors co-operate in those cases where the cephalisation coefficient in the newborn is greater than in the adult.

It is one of the merits of our late colleague, Mlle. F. COUPIN (1925), whose early death we very much regret, and ANTHONY and COUPIN (1925–26), that she, together with her teacher Prof. R. ANTHONY‡ calculated for several mammals what they called the "*indice de valeur cérébrale*," *i.e.*, the relation between the actual brainweight of a fœtus or young individual and the brainweight it should have if it were an adult of its (smaller) size.§ For an elucidation of their results I refer to *Harris*' interesting paper (1929).

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* Curiously enough the Gibbon, though sometimes grouped with the anthropoids, agrees with the Macaque in cephalisation coefficient as well as in the average brain index.

† Analogous differences may be stated among the differently cephalised animals of the other Orders, but they are not so immediately evident, partly on account of the small size of the brains, which consequently do not have many fissures, and partly on account of the more complicated character of the fissures.

‡ R. ANTHONY et F. COUPIN, 'Introduction à l'étude du développement pondéral de l'encéphale. L'Indice de valeur cérébrale pendant l'évolution individuelle,' ZAGREB, 1925–26.

§ For this calculation they rightly used the intraspecial exponent $r = 0 \cdot 25$ and the cephalisation coefficient (K) calculated from the adult, using this exponent.

From their calculations it appears that though several animals at birth have a higher relative brainweight than the adult, this is not always so, especially in anthropoids (Chimpanzee) and man. But with others, pigs and lions shortly after birth, the "*indice de valeur cérébrale*," the body brainweight relation is higher (in the pig even one and a half times larger) than in the adult. As they are also smaller than adults, both factors co-operate in making the brain rounder.

With man, it is different. Before birth, and shortly afterwards, the cephalisation is considerably less than in the adult, as first stated by Anthony and Coupin (*loc. cit.*). To test their result I did the calculation again with the same values for r ($= 0 \cdot 25$) and for K ($= 85$ for males). For the 7th and 8th intra-uterine months I used the same brainweights, collected by Ziehen (in Hertwig's 'Handb. der Entwicklungslehre'), but for the time after birth I used Pfister's figures. For the bodyweights I used the figures given by Ahlfeld from the 7th intra-uterine month till birth, and for postnatal bodyweights those collected by von Pirquet and Feer.

My results agree quite well with those of Anthony and Coupin (*loc. cit.*), and confirm their conclusion that at birth and even in the first year the relative brainweight of the child is less than it would be if it were an adult of the same size.

This, in addition to other factors (see below), may explain that notwithstanding their smaller body size the brain of human fœtuses and newborns is usually rather long.

TABLE III.

Objects.	Actual Brain-weight.	Actual Body-weight.	Calcul. Brain-weight.	Indice de valeur cérébrale.
	gr.	gr.	gr.	
7th intr. month	158·7	1,868	558	0·284
8th ,,	342·5	2,424	597	0·573
Newborn	355·0	3,768	666	0·533
End 1st month	455·0	4,400	692	0·657
,, 3rd month	515·0	6,200	754	0·683
4th, 5th ,,	573·0	7,150	782	0·733
6th, 7th ,,	734·0	8,200	810	0·906
8th, 9th ,,	752·0	9,050	829	0·907
10th, 12th ,,	832·0	9,866	847	0·993
2nd year	977·0	12,700	903	1·082
3rd, 4th year	1,150·0	15,600	950	1·211
5th, 8th ,,	1,202·0	21,625	1,007	1·193
9th, 14th ,,	1,279·0	33,833	1,153	1·109

Macalister noted the same in Egyptians and Hindus. Frasseto, who examined 156 Italian fœtal skulls, says that in the last five intra-uterine months the skull is more dolichocephalic, and in Russians Tschepourkowsky found an increasing brachycephaly in the first half year after birth (quoted from Martin). After the first year, however, there is a tendency in the human skull to elongate again (Rose, 1906;

FRETS, 1926).* As, however, the cephalisation coefficient still increases after the first year, till the third or fourth year, this again shows (*vide infra*) that in man at that period there is no such parallelism as stated above between relative brainweight and form.

If we now examine the general morphology of the newborn and infant's brain we observe features that may be partly correlated with the tendency of the brain to brachycephaly and hypsicephaly in the first year, partly with local differences in the development of the pallium.

The latter point has been examined by CUNNINGHAM (1892), and was also mentioned by MACALISTER (1898).

The general morphological features of human brains are best defined by using a set of lines and angles, which enables us to express the differences in figures—a method already used by CUNNINGHAM (*loc. cit.*) especially for the study of ontogenetic development.

I found the following standard lines and angles to be the most useful.

On the convexity we may use as a basis the *lateral horizontal* line drawn underneath the orbital operculum and the occipital pole.† This line has the advantage that it may also be drawn on endocranial casts and thus enable us to compare in some respects the braincasts of extinct and recent races (*see below*).

The additional lines on the convexity are, a perpendicular along the occipital and frontal pole, the highest possible perpendicular (which I omitted in my photographs), the perpendicular at the temporal pole, and the line along the Rolandic fissure intersecting the lateral horizontal. The Rolandic angle may be measured either behind this intersection or between this fissure and its tangent on the medial wall (CUNNINGHAM'S Rolandic angle).

A very different Rolandic angle, increasing also in shortheads, is that of CALORI, being the frontal angle on the dorsal aspect of the brain between the Rolandic sulci of both sides. The Sylvian line is most instructive if it is drawn from the point where the temporal pole intersects the lateral horizontal to the end of the Sylvian fissure. As Sylvian angle I propose to use the angle posterior to this intersection.

The basic line on the medial wall is the *ventral callosum line* running underneath the genu and splenium corporis callosi. The additional lines or measurements in the medial wall are the greatest perpendicular of the callosum drawn on this line. The greatest length of the callosum—measured from its most frontal to its most caudal end—is used in calculating the callosum index (= callosum height divided by the callosum length). Furthermore two angles, viz., the anterior angle between the basal callosum line and the stem axis (stem angle), and the posterior angle between a line indicating the main course

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* REUTER also noted a greater hypsicephaly with Pomeranian children in comparison to adults, cf. R. MARTIN, *loc. cit.*, 1st Ed., p. 606.

† CUNNINGHAM (*loc. cit.*) used a somewhat different line, viz., the greatest longitudinal axis of the brain, which, however, is not so constant.

of the parieto-occipital sulcus and the basal callosum lines (parieto-occipital angle*).

In Table IV are given some values thus obtained for newborns and for adult Dutch mesocephalics and brachycephalics.

TABLE IV.

	Newborns.	Adult mesoceph. Dutch.	Adult brach. Dutch.
Sylvian angle	45·3°	24·5°	43·0°
Rolandic angle	66·3°	54·8°	64·7°
Stem angle	95·4°	106°	96°
Par. occip. angle	47·1°	46·0°	58°
Callosum index	0·40	0·31	0·38

From Table IV we see that in the newborns the Sylvian, Rolandic, and parieto-occipital angles are larger,† and the stem angle smaller, while the callosum index is higher. The steep course of the Sylvia in newborns and the tendency of the Sylvian angle to decrease in adults has already been observed by CUNNINGHAM (*loc. cit.*, p. 133), who explained it by the further outgrowth of the parietal region after birth (a process he found more pronounced on the left than on the right). This may also explain the decrease in the parieto-occipital angle in mesocephalic adults.

Correlated with the greater steepness of the Sylvia is the big and more bluntly shaped temporal lobe, and the more transverse course of the fissures that represent the inferior temporal.

The other feature, the steepness of the Rolandic, observed by both MINGAZZINI (quoted by CUNNINGHAM, *loc. cit.*, p. 189) and CUNNINGHAM (1892), may be due to a smaller development of the frontal lobe in newborns.

In this connection I wish to draw attention to the fact that in the 7th month fœtus, fig. A, Plate 37, the junction of the inferior frontal and inferior precentral fissures lies in front of the temporal perpendicular, whereas in newborns it lies on it, and in a one and twelve months child it lies behind it, as it usually does in the adult.

With the increase of the frontal lobe in the adult this junction shifts further backward,‡ which again reacts on the Rolandic. Consequently these differences originate in intrinsic characteristics of the brain. The smaller stem angle, however, is related with the more frontal position of the foramen magnum in the skull of the newborns (BOLK).

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* For anthropological purposes this angle is the least important one as its variations in dolicho- as well as in brachy-cephalics are very large.

† I wish to emphasise that although only the best preserved brains were used for this study, changes in their shape cannot be avoided if once taken out of the skull. These changes, however, affect the dolichocephalic brains just as much as the brachycephalic ones, so that the comparison remains practically the same. Usually these three angles and the callosum index are somewhat larger *in situ*, and the stem angle smaller in both types of brains.

‡ As the temporal perpendicular tends to shift forward with the development of the temporal lobe the discrepancy between this junction and this perpendicular becomes still larger.

The high callosum index of infants, and newborns, is correlated with the relatively greater height of the brain at this period. Its later decrease may be influenced by an increase of fibres and especially by the fact that the size of the myeline sheaths in the callosum of the adults is about four times more than at birth (DONALDSON, 1912),* this chiefly affects the length of the callosum as it does in the mammalian series.

Where a lunate sulcus was evident in my specimens of newborns or infants its position was a rather frontal one and its form a pronounced vertical crescent; this may be due to the relatively further extension of the striate area on the convexity and lesser development of the parietal region.

A striking feature of the fœtal and infant's brain is the downward course of the posterior calcarine, which is later lifted up by the development of the ventral peri- and para-striate area. This also contributes to cause its dorsal hook, so frequently found in the adult. The increase of the precuneus causes the gradual decrease of the parieto-occipital angle in the adult mesocephalic (Plate 38).

Finally the large rostrum orbitale is correlated with the shape of the facies orbitalis and ethmoidalis in this period (Plate 37, B and C).

Turning now to adults we have to consider first whether or not the general shape of the adult human brain is influenced by the factors established for animals: cephalisation and body size.

As far as the first point is concerned, we can immediately leave it aside.

In the first place the differences in cephalisation in human races are too slight for us to expect them to exercise much influence on the general brain shape. This is demonstrated by the fact that, although the Australians and Negroes,† whose relative skull capacity is smaller than that of the European, are both dolichocephalic, of the two races with the highest coefficient, the Eskimos and the Japanese (DUBOIS, 1921), the former are very dolichocephalic (index 70·6–72·2: FÜRST and HANSEN), while the majority of the latter are meso- and sub-brachycephalic (index 78·3–79·3; ADACHI).

It is also striking that, whereas in the Mongols the rather small brachycephalic Buriats have the greatest brainweight (1460 gr., BUSHMAKIN, 1928), FRETS (*loc. cit.*, p. 248)‡ in 3600 Dutchmen found that the heads with high indices had on an average a somewhat smaller capacity than those with low indices.

There are various other factors that influence the general shape of the human skull (and brain), mechanical ones from muscles, ligaments, and the use of the jaw, and chemical ones (food and endocrine glands: KEITH, STOCKARD, BOLK) acting in the first place on the skeleton in general.

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* From observations by SCHLOSZBERGER.

† The difference in skull capacity between Negroes and Whites is 41 c.c.m. (*Wingate Todd*, 1923). For the Australians *see* WOOLLARD (*loc. cit. infra*) and DAVIS, TURNER, DUCKWORTH and HAUGER quoted in my 'Evolution of the Nervous System' (Bohn, Haarlem, 1929, p. 206).

‡ Speaking of the development of the human brain I have already emphasised that the increase of the cephalisation coefficient does not run strictly parallel to the increase of index.

It is beyond the scope of this communication to deal with these influences, which would require a paper of much larger size than this. They have been, however, briefly summarised by BASLER (1925) and STOCKARD (1931).

The influence of body size on the index of the skull is, nevertheless, observed with man. PITTARD* and DONICI called attention to the fact that, *ceteris paribus*, taller men tend to have longer skulls. It is also said that of all African Negro races only the Pygmies " tend to brachycephaly " (SELIGMAN, 1900).

Still the influence of body size on skull form in adult man is of little importance compared to other influences.

Whatever may be the cause or causes for the various shapes of the human skull the correlation it shows with the brain is more evident than has hitherto been realised.

In a general way differences in the brain correlated with the shape of the skull were already recognised by CALORI (1870), MEYER (1871), and RÜDINGER (1877), who called attention in a general manner to the more curved character of sagittal sulci in brachycephalics and the more frequent occurrence of transverse fissures, without dealing with the arrangement of special sulci.

ZUCKERKANDL (1883) showed the influence of early synostosis of certain sutures on the convolutional pattern, and AMBIALET (1893) described the brain form correlated with artificial deformation (*see* p. 25, and Plate 415). This did not lead, however, to a descriptive brain anthropology, probably on account of the fact that these authors had not at their disposal such a variety of well preserved brains of different races as is desirable for this purpose.

As a basis for my researches I used the fact that the population of Holland consists mainly of two groups (BOLK, 1920), a mesocephalic largely Nordic group,† and a brachycephalic hypsicephalic Alpine group, the latter occurring chiefly in the province of Groningen (DIJKSTRA, 1927).

This gave me a chance to get mesocephalic (and dolichocephalic) as well as brachycephalic brains ; the latter being also higher, more hypsicephalic than our dolichocephalic brains (and skulls).

Plates 38 and 39 show some of them. There are several striking points in these photographs.

On the convexity the following facts may be noted In the brachycephalic brains the angle between the Sylvia and the lateral horizontal (Sylvian angle) is larger than in dolicho- or meso-cephalic brains. This is correlated with a greater depth of the temporal lobe and this again with a somewhat more pronounced tendency of the superior temporal convolution to be curved and to protrude in front of the Sylvian line. Furthermore, the fissurets representing the inferior temporal show a prevailing transverse arrangement.

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* PITTARD et DONICI, " Les changements de l'indice cephalique en fonction de la taille croissante " ('Bull. de la Soc. d'Anthrop. de Paris,' 1927, p. 39).

† Prevailing in the Western provinces, especially in the province of South-Holland and further in the larger cities, Amsterdam, Haarlem, Rotterdam, Utrecht and Arnheim.

In the dolichocephalic brains the inferior temporal consists of rather longitudinal grooves. I also call attention to the long prelunate sulcus (P—P) in the second dolichocephalic in Plate 38.

Another feature in brachycephalics is that ELLIOT SMITH's lunate sulcus, if present, has often the shape of a high, vertical crescent than in dolichocephalics, and thus may resemble more the simian shape. Postauricular shortness of the skull, together with its greater height, seems to be responsible also for these features. Furthermore CUNNINGHAM's Rolandic angle (the frontal angle between the Rolandic fissure and its tangent on the dorso-medial wall) as well as my Rolandic angle (between this fissure and the lateral horizontal) are larger in the brachycephalics ; a result of the greater steepness of the central sulcus.

That this is also correlated with the postauricular shortening and greater height appears from the fact that while the ventral end of the central sulcus practically has the same topographical relation in both sorts of brains its upper end has shifted somewhat forward in brachycephalics, a fact important for cranio-cerebral topography and well known to brain surgeons.

Other features correlated with the postauricular shortening are the sharper curve of the intraparietal and the more constant development of the so-called ascending branches of the superior temporal, the angular, the r. ascendens temp. sup. proper and the anterior occipital sulci of SHELLSHEAR (1927).

But this is not conspicuous on the photographs which should for this purpose have been taken from another direction.

On the frontal lobe the differences are not so striking. Still the three sagittal fissures are easier to study, especially the midfrontal in dolichocephalics.

On the mesial side the stem angle in brachycephalics is smaller than in dolichocephalics. As this angle is so easily changed during fixation outside the skull I added a photograph of a brachycephalic and a dolichocephalic* brain in the skull. From this, as well as from the other brains, it appears that in the brachycephalic skull this angle is smaller than in the dolichocephalic ones. As in newborns (*vide supra*) this feature is correlated with the position of the foramen magnum, which in brachycephalics lies further forward than in dolichocephalics (BOLK, 1907). Correlated with the smaller stem angle is the narrow fossa interpeduncularis in brachycephalics and—less constant—a shorter pes pedunculi.

The greater callosum index in brachycephalics is also to be explained by the greater height and occipito-frontal shortening of the brain.

As stated above the parieto-occipital angle varies so much in dolicho- as well as in brachy-cephalics that it is difficult to make a reliable general statement. In brachycephalics, however, the parieto-occipital angle may be enlarged by the occipital shortening, which also causes the occipital lobe to turn down more steeply than in dolichocephalics. A feature often correlated with this is the sharply hooked form of the posterior calcarine fissure, described in East European brains by WEINBERG (1898),

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* This is an English brain. I am indebted to Prof. WALMSLEY of Belfast for giving me the original photograph of this skull (index 70), already published for SYMINGTON (Edinburgh Medic. Journ., 1915).

and in Chinese brains by DR. VAN BORK. In the first and second brachycephalic of Plate 39 this fissure shows a sharp arch that has even acquired a processus acuminis. The same process may lead to a higher insertion of the posterior calcarine on the parieto-occipital (*see* the second brain). Although a curved calcarine is not uncommon in dolichocephalic brains also (*cf.* the Soudanese brains below) it seldom forms such a sharp hook.

Another feature frequently observed in brachycephalic brains is the oblique course of the ascending branch of the calloso-marginalis.

While in the photographs of the second and third dolichocephalic this part of the callosomarginalis runs nearly perpendicular on the mesial edge of the hemisphere, in brachycephalics (Plate 39) it frequently approaches the mesial circumference in a frontally wider arch. This is rather peculiar, as the postauricular shortening of such skulls is frequently correlated with a steeper parieto-occipital. The more frequent oblique course of the ascending branch of the calloso-marginal may be explained, however, by the very fact that the occipital shortness of the brain causes the precuneus to shift forward, wedging in between the callosum and the ramus ascendens calloso-marginalis and thus lifting up and stretching the latter.

This shifting of the precuneus may be expressed in another way, suggested by CUNNINGHAM, who measured what he called the parietal and occipital indices by comparing, on the mesial edge, the distance between the Rolandic and occipito-parietal indentations on one hand, and the distance between the latter and the lower edge of the occipital lobe on the other.

Applying this method to my Dutch brains I find this relation to hold in the mesocephalics (with great variation) 5·2 (occ.) : 5 (par.), in the brachycephalics 5·2 (occ.) : 4·2 (par.), thus showing that the parietal region in the latter is compressed. As the parietal region extending between the indentation of the central and the parieto-occipital practically coincides with the precuneus (and a small part in front of it) this also proves the frontal displacement of the parietal region.

The differences mentioned are not always equally evident, nor all present in the same specimens, but making averages of a large number of each of the two groups of brains they come out quite clearly.

Proceeding to the relations in other human races, I shall discuss chiefly the brains of such races as I could examine myself. I shall begin with the brain of nine Armenians, a hyperbrachycephalic, hypsicephalic race.

On the convexity of the brain, illustrated in Plate 40, the large Sylvian angle strikes us at once. The average is 40°. This is correlated with a deep temporal lobe that shows a tendency to a prevailing transverse fissuration underneath the superior temporal. The superior temporal convolution itself is strongly curved, frequently interrupted, and protrudes in front of the Sylvian line (*see* specially brain B, Plate 40).

These features are apparently correlated with the striking postauricular shortness and occipital flattening so peculiar to the Armenian skull, which also causes the central sulcus to run steeper, the average of my Rolandic angle being 70°.

The lunate sulcus, when present, has a perpendicular position.

The same influence is evident on the mesial wall. This is observed in the third brain C, an old brain, apparently fixed in the skull. The stem angle of this brain is small (97°), the fossa interpeduncularis narrow, the parieto-occipital angle rather large (47·5°), and the callosum very high (its index being 0·4). The ascending branch of the calloso-marginal fissure finishes with two branches, one of which runs horizontally, the other in a curve to the mesial edge of the hemisphere. The occipital lobe runs down steeply and the posterior calcarine shows a sharp dorsally pointed hook, and in addition has a high insertion on the parieto-occipital.

The fourth Armenian brain (D) reproduced here was deformed during transport. The occipital lobe is lifted up and the stem angle enlarged. The deformation, however, does not, or at least hardly, affects the Sylvian and Rolandic angle. Both of these are large, the former being 46·5°, the latter 77°. As in the other Armenian brains the temporal lobe is big, the region underneath the superior temporal tends to make transverse sulci and the superior temporal convolution is considerably curved and protrudes in front of the Sylvian line.

The callosum is still high (the index being 0·39). The posterior calcarine, although stretched out by the lifting up of the occipital lobe, still shows its dorsal hook and high insertion.

The lunate sulcus (*l*) in brains A, B and C (Plate 40), has a pronounced perpendicular position. In other words the Armenian brains show the same characteristics as the Dutch brachycephalics, but to a greater extent.

Proceeding from the Armenians to the Lebanese we turn from a Caucasian-speaking people to an Arabic-speaking one. The Lebanese consider themselves to be Arabs. There are, however, good reasons for believing that they belong to the same ethnic group as the Armenians, the ancient Subarean or Ponto-Zagrian group.

In fig. 1 I give a curve of the cephalic index of 138 Armenians (continuous line) superposed upon a curve of 200 Lebanese (dotted curve).

From this it appears that not only are both prevailing brachycephalic but their index curves also run parallel, and that two peaks, one at 83–84 and one at 86 occur in both curves, a phenomenon similar to that found in the Armenians by CHANTRE (1895), BUNAK (1927) and by Dr. and Mrs. KRISCHNER (1932).

Further, the height indices of the head are nearly the same in the Lebanese and Armenians and so are the blood indices (*see* Table V).

The chief difference between the Lebanese and Armenian index curves is that the index curve of the Lebanese has an additional peak which does not occur with my Armenians. This additional peak is apparently caused by an admixture with the population of the cities lying between the Lebanon and the desert.

Superposing the index curve of the people I measured at Damascus, Ma'allullah and Homs, on the Lebanese index curve, fig. 2, it appears that the chief peak of the curve of the desert border people coincides with the additional peak of the Lebanese curve. That both are very different from the Adnan Arab group of the North Syrian desert appears from fig. 1, in which I added the index curve of 101 male Bedouins of the Syrian desert (dotted-striped curve).

I could only get one Lebanese brain (Plate 40) at the bottom (E, Mahmoud Hassan, ceph. index 83·5). If, however, we compare this brain with my fourth Armenian brain* (Kalajian) it appears that they are very much the same, so much indeed, that if I did not keep them well labelled I would mistake one for the other.

Notwithstanding the deformation in both brains the depth of the temporal lobe is still very considerable. The Sylvian angle in the Lebanese is large (42°). The superior temporal convolution is strongly curved and frequently interrupted, and the inferior temporal consists of various transversely disposed fissurets.

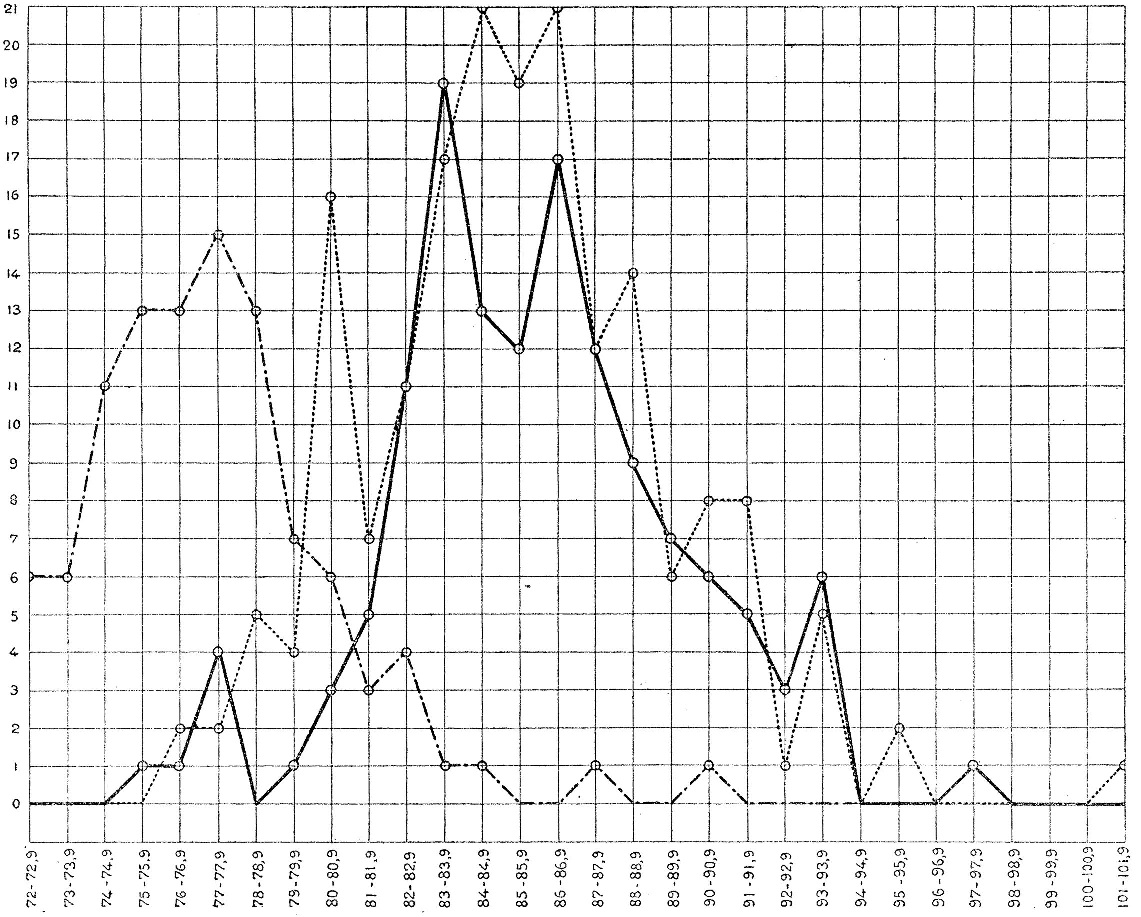

FIG. 1.

Another feature occurring equally in the Armenian as well as in this Lebanese brain is the steepness of the central fissure (the Rolandic angle being 68°).

To these characteristics I may add that the parieto-occipital angle is large (an observation made on the fresh brain). The precuneus is small, the ascending branch of the calloso-marginal runs more oblique than in the Armenian brains.

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* I compare it especially with this Armenian brain as both brains were deformed during transport to about the same extent.

The artificially stretched posterior calcarine has a very high insertion on the parieto-occipital—a feature that is parallel to a calcarine hook. *In situ* the callosum index must have been large in my Lebanese, as even in the flattened condition in which the brain arrived it is still fairly high (0·367), just as high as with the fourth Armenian brain which is about equally flattened.

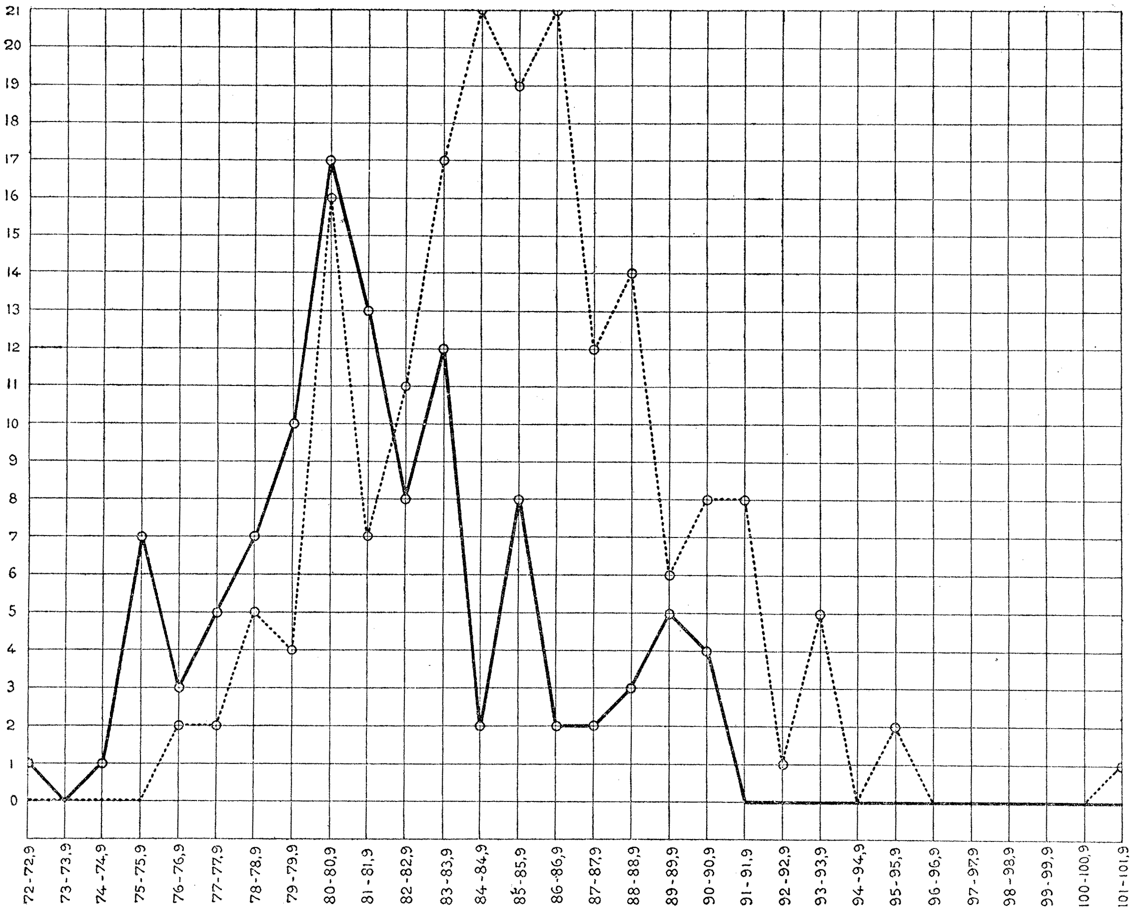

FIG. 2.

Although I had only this Lebanese brain at my disposal its fissural features, connected with its brachy-hypsicephalic Armenoid character, are so evident that I could not omit describing it. Also the blood index of the Lebanese, 2·56 according to PARR'S (1929, 1930)* researches, comes very near the blood index of the Armenians (2·31), whereas the blood index of the Syrian Adnan Arabs is about 1·59.

As stated above (*cf.* figs. 1 and 2) the cephalic index of the Adnan Arabs differs very much from that of the Armenians and Lebanese. In Table V their average measurements and indices are compared with those of the Armenians and Lebanese :

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* For the Lebanese blood index his figure for the Maronites is taken, as the majority of them are Lebanese.

TABLE V.

Races.	l.	br.	h.	l.br.i.	br.h.i.	l.h.i.	Blood index.
Syr. Bed.	18·71	14·38	12·7	76·85	88·3	67·9	1·59
Leban.	18·19	15·44	13·26	84·88	85·87	72·1	2·56
Armen.	18·20	15·54	13·13	85·38	84·49	72·14	2·31

I have not been able to get an Adnan Arab brain, but on account of their prevailing mesocephalic index we have reason to believe that its fissuration differs from the Lebanese.

The only description of an Arab brain from Arabia,* given by COLE (1920), seems to confirm this supposition.

The form of this brain is no more the natural one. The deformation has exaggerated the horizontal course of the Sylvian fissure and the small depth of the temporal lobe.

The longitudinal, and especially the uninterrupted character of the inferior temporal, cannot, however, arise from post-mortem pressure, nor the distinct character of the midfrontal sulcus.†

Typical examples of long-headed brains, more easily obtainable, are those of the Egyptian (Hamitic) Fellaheen (ELLIOT SMITH, 1914, 1923) and Soudanese brains.

Prof. D. DERRY of the Government Medical School at Cairo kindly fixed two Fellah brains for me in a manner suitable for anthropological research. I reproduce photographs of them in Plate 41. The stem angle is large (somewhat enlarged ? average 117°), the Rolandic angle is small (52·3°), the Sylvia runs very straight and the Sylvian angle (average 28°) is small. The superior temporal presents a simpler and straighter course, curving only at the temporal pole.

This downward curve is very obvious in all the four Fellah hemispheres. It does not so often occur in such a continuous form in Dutch longheads nor even in Soudanese, Hereros, or in American Negroes, although POYNTER and KEEGAN found an independent temporalis transversus in front of the superior temporal in 65 per cent. of these brains, anastomosing occasionally with the superior temporal. This independent curve is more frequent still in brachycephalics. The continuous frontal curve is also evident in TIEDEMAN'S "Hottentot Venus" and in several Australian brains. It seems well worth while to trace this feature in a larger number of Egyptian brains. It possibly is a rather primitive arrangement, and is also observed in anthropoids, and may be present in some Neanderthal casts.

Also in the inferior temporal region a longitudinal arrangement of fissurets prevails.

In Plate 41 I reproduce the Soudanese hemispheres, also fixed for me by Prof. DERRY. These brains again have a large stem angle (117·3°), a small Rolandic (50·3°) and Sylvian

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* In Arabia proper, especially in Yemen and also Oman, a good many brachycephalic Kohtan Arabs occur, but this brain was dolichocephalic. In this Arab, COLE suspected some admixture with Negro blood.

† I hold that in COLE'S figure 18, showing the convexity of the frontal lobe, the upper arch 15 connecting with 14 is my 6, while his tri-radiate sulcus 10 (above his 8) is my 8. (COLE'S figures indicate the depth of the Sulci in m.m.g. but I have no other means of referring to them.) Also in this brain the midfrontal is rather primitive.

angle (28·3°). The small depth of the temporal lobe (already emphasised by PARKER (1879) and BEAN (1906) for the American Negroes) and the more pronounced tendency of the inferior temporal to form longitudinal fissurets are equally striking ; I want to call attention also to the very straight course of the Sylvia (*see* especially the left photograph at the bottom) ; a point noted also by POYNTER and KEEGAN (1915) in the American Negro. For a further discussion of these and related brains I refer* to page 421. I cannot, however, leave these brains without stating that the parieto-occipital is rather steep, and that the posterior calcarine in two hemispheres is obviously curved and inserted higher. These features are usually not found in dolichocephalics.

Analogous relations seem to occur in the drawings or photographs of other dolichocephalic races, such as Eskimos (*cf.* the illustrations published by HRDLIČKA (1899, 1901) and SPITZKA (1902)) and Australians (*cf.* the papers of FLASHMAN (1903, 1908, 1916), DUCKWORTH (1908) and WOOLLARD (1929, 1931)).

In this connection it is well worth while to mention here some peculiarities found in the dolichocephalic Australian aboriginals, and described by the two last-named authors. Returning later to the midfrontal, evident in six out of eight hemispheres, described by DUCKWORTH (and shown in his pictures), and in all the brains described by WOOLLARD, I here only want to state that in WOOLLARD's brains (1 and 2), fixed *in situ*, the Sylvian and Rolandic angles are very small and consequently the depth of the temporal lobe. This latter shows little transverse fissuration of the inferior temporal convolution.

Although WOOLLARD and also DUCKWORTH are inclined to recognise a lower or more primitive† organisation in this brain, with which I agree, WOOLLARD rightly emphasises that several fissural features in the Australian aboriginal brains may be explained by the dolichocephaly of these subjects (for his interesting remarks concerning the temporal region, I refer to page 424).

In the preceding pages we have seen that some fissural features established for the two main skull forms of the Dutch may be traced also, and even in a more obvious way, in other races with similar or more pronounced skull features.

Hitherto I have compared brachy-hypsicephalic with meso-non-hypsicephalic brains.

I shall now turn to two other anthropological brain-forms and discuss the influence of brachycephaly not combined with hypsicephaly but with platycephaly, and the influence of hypsicephaly not combined with brachycephaly but with mesocephaly.

As is well known, anthropologists usually divide the Mongol races into two main groups : the brachy-platycephalic Northern Mongols and the mesohypsicephalic Chinese

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* For racial peculiarities of the Sudanese people and related races I refer also to ELLIOT SMITH, 'The Archeological Survey of Nubia,' Report for 1907–1908, vol. 2, Report on the Human Remains.

† Their arguments for this are, *e.g.*, a more frequently exposed insula, the more constant occurrence of the lunate and paracalcarine and the lesser fullness of the frontal lobe, while WOOLLARD emphasised the poorer development of the cortex, especially in the acoustic area. The last argument certainly is the stronger one.

group. With the former the length-breadth index of the head varies between 84 and 89, the breadth-height index between 85·9 and 87·5 (REICHER, 1913). Whereas with the second group, the Chinese, the values for the average length-breadth index are lower (about 78·5), those for the breadth-height index are considerably higher, varying between 97·7 and 100·2 (KOGANEI, 1902).

These relations are, of course, reflected in the general form, but they also appear in some special features of the brain. Although the material for the study of the Northern Mongol brain is very scarce, it seems to show the features that may be expected with such skull forms. Plate 43 is a photo of a Mongol brain received from Prof. STEFKO, and the excellent drawings made by G. RETZIUS (1891) in his description of the brain of a Lapp (average l.b. index of 19 skulls measured by RETZIUS : 86·3). In these brachy-platycephalic brains the following features occur. Although the Sylvian angle is not large, as may be expected in a flat skull, it is larger than in the mesocephalic and dolichocephalic brains hitherto discussed, and the temporal lobe shows a prevailing tendency to transverse fissurets underneath and above the superior temporal. The Rolandic angle, however, is smaller than in brachy-hypsicephalic brains, which is also an expression of the flattening of these brains, as the upper end of this sulcus lies far backward.

On the mesial surface of RETZIUS' Lapp we find the small stem angle, narrow fossa interpeduncularis and short pes as an expression of brachycephaly. On the other hand the parieto-occipital angle in both brains is large and the calloso-marginal ends in an obliquely running branch.

The callosum is not nearly as high as in the brachy-hypercephalic Armenians. Consequently the features correlated with brachycephaly are evident only so far as the platycephaly does not prevent them from emerging. More brains of the Northern Mongols, however, are necessary to verify these points.

The greatest number of Northern or Central Mongol (Buriat) brains (35) have been examined by BUSHMAKIN (1928). From his rather brief and not amply illustrated paper I have already quoted (*see* p. 402) the high brain weight for these people. This material, together with the 26 brains weighed by TALKO HRYNTZEWITSCH gave an average weight of 1485 gr. for the males and of 1438 gr. for the females. This is the more striking since the average stature in this group is smaller than that of the Russians, used for comparison, whose brain weight was not as high.

As far as the fissuration is concerned he also mentions the frequent interruption in the inferior temporal, and the prevailing deep transverse fissures in the occipital region, so that the transverse occipital frequently connects with the superior temporal, a feature rarely found in dolichocephalics. On the other hand, the midfrontal fissure seems to keep (more frequently than in the Chinese) its classic arrangement. It may be that this is correlated with a frontal flatness of the skull (*see* p. 413).

We now come to brains which on the whole are not brachycephalic, but whose relative height is the predominant feature : the Chinese brain (Plate 44).

In the last few years KURZ (1924), I, and especially Dr. VAN BORK (1930) examined a large number of Chinese brains, partly from Peking, partly from Hong-Kong. For the latter we are much indebted to Prof. SHELLSHEAR. I shall mention here only the main points found in connection with the problem under discussion, and I shall illustrate these by photographs of three Chinese brains (Plate 44). Other illustrations may be found in the literature quoted.

Among the more than seventy Chinese brains examined, a special group of brains struck us by certain constantly recurring features. In order not to prejudice its ethnic relation we called this the A group, and it is this group to which I now refer.

As the Chinese are mesocephalic—at best sub-brachycephalic—we find some points in their brains in which they rather agree with the mesocephalic Dutch, *e.g.*, the Sylvian angle (mesoc. Dutch 24·5 ; Chinese 31·1 ;* hyperbrachycephalics 41·6†) and the parieto-occipital (mesoc. Dutch 46° ; Chinese 49° ; hyperbrachycephalics 58·7°).

The antero-posterior compression of so many Chinese skulls, however, appears in the smaller stem angle (mesoc. Dutch 105° ; Chinese 97° ; brachycephalics 96·2°), small fossa interpeduncularis (already observed by KURZ), and higher callosum index (mesoc. Dutch 0·30 ; Chinese 0·36 ; brachycephalics 0·4) ; *cf.* also Dr. MA WEN CHAO (1927). So in these points they rather resemble the brachy-hypsicephalic Dutch.

Apparently the features characteristic of these brains concern more the top parts of it, so the oblique course of the ascending branch of the calloso-marginal occurring with brachy-hypsicephalics is frequent here also, and the Rolandic seems to run a good deal steeper than in mesocephalic Dutch brains (Rolandic angle of the mesocephalic Dutch 54·8°, the Chinese of type A 66·6°‡, hyper-brachycephalic Dutch and Armenians 65·7°). Furthermore Mrs. VAN BORK emphasised the frequent occurrence of a sharply hooked posterior calcarine in this type of brain as a consequence of its flat-occipital shape, while the downward curve of the occipital lobe also affects the basal, occipito-temporal region by frequently causing a transverse fissure (v. BORK's fiss. basalis transversa).

Also the steepness of the hippocampus emphasised by KURZ, and confirmed by us, may be correlated with the general shape of the skull, that may even explain the interesting feature observed by Mrs. v. BORK, viz., that the lunate sulcus in these brains usually has the position of a vertical crescent,§ while in the mesocephalic Dutch it tends to flatten out (VAN BORK, *loc. cit.*, figs. 25 and 27 ; *cf.* also the description by SHELLSHEAR (1926)).

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* Dr. A. VAN BORK-FELTKAMP, who measured 16 Chinese brains of the A type, found an average only 27·5°.

† This figure is the average of hyperbrachycephalic Dutch and the Armenians photographed in this paper.

‡ Mrs. VAN BORK, measuring this angle on the brains themselves, found an average of 65·3 in fifteen Chinese brains of the A type.

§ The material used for STEFKO's interesting paper, " Cytoarchitektonik der Regio Rolandica, frontalis, area striata und opercularis bei den Chinesen," seems not to be sufficiently well preserved in all respects to allow a conclusion (*see* ' Z. Ges. Anat., vol. 81, 1926).

It is on account of these facts that KURZ found the Chinese brain to resemble more or less the (very brachycephalic) Orang-Utan brain, and tried to trace the origin of the Mongol race from this anthropoid, a statement not based on sufficient evidence, although the polyphyletic origin of the human race is accepted by authors like MELCHERS and KLAATSCH.

The frontal lobe of these Chinese brains strikes us by the height of its slope. This is obvious if we compare it with Dutch or Japanese mesocephalics. The Chinese frontal lobe is somewhat less semicircular, but has some resemblance to a highly curved nose, an appearance correlated with the fact that the facies orbitalis of the skull is fairly high and has a more oblique or vaulted shape than in other meso- or sub-brachycephalic skulls, *e.g.* the Japanese (and Dutch). As a consequence the thinner lower part, the rostrum of the frontal lobe, is more evident in the Chinese, a feature already noted by PARKER and MILLS (1886) and by DERCUM (1889, 1892).

The average of the Japanese skull is slightly less mesocephalic than the Chinese. ADACHI gives the Japanese an index of 78·3 for the males and 79·3 for the females; others give it a slightly higher index, 80·82. Thanks to the kindness of Professor G. FUSE, in Sendai, I had at my disposal eight brains from Japan, all of them well fixed. In Plate 45 I give photographs of three of these brains. In all my specimens the following points may be seen:—

The Sylvian angle is less small (average 31·5°) and the superior temporal convolution in all cases has a distinct frontal curve, though less so than in distinct brachycephalics. Corresponding with these facts the temporal lobe is somewhat larger in dorso-ventral dimension and its fissuration tending more to transverse fissuration than in the Chinese. Concerning the Rolandic angle (average 64°) I should not like to make any statements.

The rounder form of the frontal lobe as compared to the Chinese is evident on first sight in all my eight specimens; it may be more emphasised by connecting the temporal perpendicular, where it intersects the dorsomedial edge of the brain, with the most frontal point of the frontal lobe.

The angle thus formed with the temporal perpendicular is constantly larger in my Japanese (average 40°) than in my Chinese brains (average 35°). The same is seen in the three Japanese brains described by SERGI (1913).

This is in harmony with the greater height of the Chinese head and with the fact, observed by BÄLZ (1880), that the Japanese front tends to protrude, a feature rarely occurring with the Chinese, *cf.* HABERER (1902) and MOCHI (1908). On the mesial side the high callosum index and small stem angle (average 96°) are equally striking, as in the Chinese.

I finish this part of my paper by showing some brains of Bataks, a people usually considered as belonging to the Protomalay or Indonesians of HAMY (1926), together with the people of Mentawei and Nias and the Dajaks (KLEIWEG DE ZWAAN (1925)).

HAGEN (1890) and VÖLZ (1900) pointed out that their cephalic indices show a similar numerical relation of dolicho-, meso- and brachycephalics as the Nias people, so well described by KLEIWEG DE ZWAAN (1914, 1915). According to the latter (personal communication) they have to be considered as being largely a mixture of Proto- and Deutero-Malay with the Vedda element. Brachycephaly is rare with them, the longheads being predominant. By the kindness of Dr. DE HAAS, who at that time practised among them as a physician to the Hospital of the Batak Institute, I recently got 16 very well fixed Batak brains.

Leaving the detailed description of this precious material to Dr. VAN BORK I only want to give the photographs of male and female Toba-Batak and male and female Karo-Batak brains (Plate 46).

Whether as a rule the women among this people tend more to brachycephaly than man, I do not know.

It may be just fortuitous that in both the cases represented here the female brain was brachycephalic, the male brain mesocephalic (the male Toba brain, No. 938, even dolichocephalic).

I refer to these specimens only because they show that the features characteristic of other races with similar indices also occur in them.

The female brachycephalic brains have a steeper Rolandic and Sylvian angle, and a deeper temporal lobe. In the brachycephalics the inferior temporal consists of transverse fissurets, while in the dolichocephalics the inferior is stretched. The brachycephalics have a more pronounced rostrum, the stem angle is smaller, the callosum index distinctly higher.

Of the two Toba brains the brachycephalic one has a larger parieto-occipital angle. This does not hold good for these two Karo-Bataks, but the occipital pole in the mesocephalic man is slightly lifted up so that in this specimen the large value of this angle is not reliable.

The calcarine in both mesocephalics is obviously curved, but the curve is not a sharp hooklike one. On the other hand, this fissure in the brachycephalic Toba woman is straight, but shows a higher insertion on the parieto-occipital fissure, while in the brachycephalic Karo woman a sharper angle in the calcarine is at least indicated.

For detailed descriptions of these and other aboriginal brains of the Indian archipelago I refer to the papers of BOLK (1905), KOHLBRUGGE (1906, 1909) and KOOY (1921). The latter pointed to the frequent occurrence of the lunate sulcus, which in some cases seems to lie rather frontally, correlated with a further extension on the convexity of the striate area, a feature mentioned by BRODMANN (1909, 1913) and VAN NOORT (*loc. cit. infra*). According to ELLIOT SMITH (*loc. cit. supra*) the same occurs in the Egyptian Fellaheen, while BRODMANN found it in Hereros. This feature cannot be so readily related with the skull form (see p. 415 and 416).

I cannot refrain from adding another picture of a Karo-Batak brain (Plate 47, B), which apparently comes from a bathrocephalic skull, a Dutch example of which is shown in Plate 47 A.

Bathrocephaly occurs with various races, although, as it seems (MARTIN, 1st edition, p. 719), more frequently in brachycephalics. In England PARSONS (1908) found it in no less than 8·6 per cent. of mediaeval skulls from Kent. Dutch bathrocephalic skulls have been described by BOLK (1915), who was inclined to explain the disharmony between the basis of the skull (including the squama of the occiput) and the rest of the neurocranium by a different heredity for the basal and upper parts of the skull.

Whatever may be the cause of this peculiarity, the way the brain may adapt itself to it is rather interesting and very striking in my case, as the tendency to a transverse fissuration in the shorter upper part and the typical longitudinal arrangement in the lower occipital lobe, corresponding with the elongated squama, is evident.

In artificial deformations of the skull analogous correlations are described in a general way by ECKER (1876) and in more detail by ZUCKERKANDL (*loc. cit. supra*) and AMBIALET (*loc. cit. supra*). For our purpose the work of AMBIALET is especially interesting as it confirms one of the theses defended here to account for racial skull variations: viz., tendency of the mid-frontal to be more regular and continuous in non-hypsicephalic, frontally sloping skulls. Plate 47 shows some figures of the skulls and corresponding brains. In the frontally sloping brain (F) the continuity of the mid-frontal (7) and its connection with the fronto-marginal (9), and backward with the precentral (5) by means of arch 6 is evident. This is, so to say, an experimental proof of our anthropological deductions.

From the brains of various races already mentioned it would appear that not only the general shape of the brain, as is self-evident, may be correlated with the racial type of the skull, but that a number of fissural and other details are apparently also correlated with it, and so do not necessarily involve intrinsic cephalic differences.

There are, however, several fissures that do not show such a correlation with the skull-type and other fissures, the form or the location of which may even be the opposite to what might be expected from the skull form.

It is evident, therefore, that in such cases we may have more really primary intrinsic cerebral differences, if at least the arrangement referred to is statistically corroborated. For this it will be necessary to examine a larger number of brains of most races than has hitherto been available.

Of such fissures I mention the posterior rhinal sulcus, the anterior branches of the Sylvia and the lunate sulcus (in Australians especially).*

As far as the Negroes are concerned several primitive features may be added to the already primitive, *i.e.*, highly dolichocephalic shape of their skull and brain, and its, perhaps, slightly lower relative capacity (TODD, 1923, TODD and LINDALA, 1928), according to BENNET BEAN (1906) in the frontal lobe especially.

As features that cannot be due primarily to the skull-type, I may mention that ELLIOT SMITH and BURNE (1902), and ELLIOT SMITH (1907) found the lunate sulci more symmetrical in the Soudanese than in other brains and the posterior rhinal sulcus quite

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* Probably also the parietal region should be included here, but notwithstanding some statistical relations for the Dutch collected by WANG HWEI WEN and myself (*loc. cit.*) and the relevant evidence collected by SHELLSHEAR (*loc. cit.*), I am not prepared to give any racial evidence here apart from skull influence.

often in Soudanese, but not in Europeans. The latter feature may run parallel to the constant occurrence of a rhinencephalo-temporal convolution, mentioned by SERGI (*loc. cit.*).

Furthermore WALDEYER (1894, 1906) found the anterior horizontal branch of the Sylvia "frequently absent" in his Negro-brains.

In the American Negro POYNTER and KEEGAN (*loc. cit.*) found the anterior branches of the Sylvia more often arranged in Y form, a statement confirmed by GENNA's observation (1924–5)* on eleven aboriginal brains from the Cameroons, but not by SERGI's observations on Hereros.

If WALDEYER, POYNTER and KEEGAN, and GENNA, who together examined more than 50 brains, are right, this relation cannot be associated with, or at least not caused by, the skull, as from a mechanical viewpoint a dolichocephalic frontally sloping skull would favour the separation of the rami anteriores Sylvii; while a frontally shorter, less sloping skull would keep these branches together (*see also* AMBIALET's figures in Plate 47). Besides, the intrinsic value of the occurrence of both anterior branches of the Sylvia is proved by the fact that in Europeans a single—or poorly bifurcating—r. anterior Sylvii, occurring in 41 per cent. on the right, is found in only 11 per cent. on the left (CUNNINGHAM, *loc. cit.*, and QUANJER, *loc. cit.*). Numerical relations for both hemispheres are desirable also for Negroes and Australians.

In the Dutch a more frontal position and typically transverse location of the lunate sulcus is less frequent with long heads than with short heads, as may be explained by the skull. In the Negro, however (BRODMANN, *loc. cit. supra*), and also as it seems in the Egyptian and Australian, the lunate frequently extends rather far on the convexity (to the lambdoid suture, SHELLSHEAR)†, and the same has been observed in Egyptian Fellaheen by ELLIOT SMITH (1904) and in the Madurese by VAN NOORT (*loc. cit. infra*).

Although a larger number of brains is necessary for reliable statistical figures, such facts—not generally correlated with skull form, or even the reverse of what might be expected in such skulls—are the most valuable ones for anthropological studies on the brain.

The question becomes much more difficult if a primitive arrangement may be correlated with the primitive frontally sloping skull alone as well as with a primitive encephalic relation, as is the case with the frontal and temporal sulci.

In order to trace the latter we have to start with the brains of extinct human races.

To begin with a few words concerning the possibility of using the lines applied in this paper for the study of prehistoric brain casts. With endocranial casts we can only have an opinion concerning the markings on the convexity; the study of the mesial surface is, of course, impossible.

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* For mental capacities of Negroes *see* DAVENPORT, "Do Races Differ in Mental Capacity?" ('Human Biology,' vol. 1, 1929).

† Personal communication.

But even the study of the convexity is much hampered by the fact that only some parts of the endocranial casts show ridges and indentations of fissures.*

These are the orbital, frontal occipital and (usually to a smaller extent) also the temporal lobes. On the centro-parietal lobes only the impressions of the arteries are distinct, and it is by its supposed more or less constant relation to these arteries that the position of the lower end of the central sulcus may be guessed.

Sir ARTHUR KEITH (1929)† has explained this particular characteristic of the centro-parietal lobe by the fact that this part more than other parts is separated from the skull by cerebro-spinal fluid, which may be due to the specific weight of the brain being slightly higher, so that in the erect position of man the orbital surface of the skull is most apt to receive impressions and, by sideward pressure, the lower temporal parts (*cf.* also SYMINGTON, 1915), and the lower frontal and occipital parts.

Although according to SYMINGTON in recent skulls the course of the Sylvia is frequently fairly well marked in casts of prehistoric skulls, usually the upper part of the Sylvian fissure can only be guessed and consequently here our lines and angles are of no help.

Only the lateral horizontal can be drawn in several casts with fairly great accuracy, for, as pointed out by SCHWALBE (1904), the third frontal convolution forms an evident marking on the endocranial (and external) surface. Similarly the ventral pole of the occipital lobe. As in several cases the anterior temporal pole is indicated on the cast, the temporal perpendicular may be drawn with a fair amount of accuracy.

The temporal perpendicular, however, has not such a constant relation to the other parts of the brain‡ although the relief the temporal convolutions may give, even on the outside of the skull, is very conspicuous (SCHWALBE, 1907).

But, " si l'on n'a pas ce qu'on aime, il faut aimer ce qu'on a." Yet it appears that these two lines may be of some use in estimating homologies, especially of the frontal fissures, in such casts.

Although it does not provide new facts, it nevertheless gives new proof of the correctness of the fissural homologies stated by Sir ARTHUR KEITH and by myself in various prehistoric brains, *e.g.* in that of *Pithecanthropus*. Besides it may help us in doing away with misinterpretations concerning the homologies of the frontal fissures in anthropoids and man.

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* I need not here enter again into a discussion about the value of endocranial indentations for the study of fissures, doubted by SYMINGTON. In this respect I quite agree with BOULE and ANTHONY (1917), ELLIOT SMITH and KEITH. Occasionally even all the sulci, including those of the centro-parietal region, are shown on an endocranial cast, as appears from a cast in Prof. A. FR. DIXON's department in Trinity College, Dublin.

† *See also* A. KEITH. A report on the Galilee skull in 'Researches in Prehistoric Galilee,' by F. Turville Petre, 1925–1926, Brit. School of Archæology in Jerusalem, London, 1927.

‡ A more constant mark in this respect might be the perpendicular on the lateral horizontal running immediately in front of the chiasma, but, in few skulls is the base sufficiently preserved to show this particular point.

Dealing with the nearest relative of man, the Chimpanzee, I may call to mind that there are only two *constant* sagittal sulci on the frontal lobe (indicated in Plate 48).

With few exceptions these sulci are called the first or superior and second or inferior frontal (KÜKENTHAL and ZIEHEN, 1895). While the homologisation of the first frontal sulcus in anthropoids with the human superior frontal is correct, the statement of various authors (KÜKENTHAL and ZIEHEN *loc. cit.*), BOLK (1901, 1909) and recently MINGAZZINI (1928, pp. 210–11), that the second frontal sulcus of apes is the homologue of the human inferior frontal, is wrong, as appears from the following facts.

If we compare the endocranial cast of the *Pithecanthropus* of DUBOIS with the Chimpanzee brain (*see* Plate 48), there seems to be little doubt that the two frontal fissures (11 and 7), so distinct in the Chimpanzee, also occur in the *Pithecanthropus* cast, which, also in other details of its frontal fissuration, has distinctly chimpanzoid features*, *e.g.* in the transverse fissures between 7 and 11, the relation of the fronto-marginal 9 to 7 and of the fronto-orbital or sub-frontal sulcus (1). Even the small independent dimple 8 (a very frequent feature even in man) is nearly identical in both.

Moreover, it appears that in *Pithecanthropus* underneath 7 another fissure (4) occurs which runs in an archlike way. On the left hemisphere of *Pithecanthropus* it runs somewhat steeper still, its course resembling more the relation of fissure 4 ? in my Chimpanzee, which may be its primitive homologue, also on account of the fact that the junction of 4 and 5 (= inferior precentral) in both falls exactly on the temporal perpendicular† (which covers 5 in the Java ape-man).

Fissure 4 of *Pithecanthropus*, however, is clearly the homologue of the human inferior frontal, a statement made by Sir ARTHUR KEITH and by myself, independently of each other. Dr. NAGTEGAAL (1929) happened to find a perfectly identical arrangement of the inferior frontal in a microcephalic idiot.

Furthermore it is evident that fissure 7 in this Chimpanzee and in *Pithecanthropus* is the homologue of the Neanderthal and recent human midfrontal.

A typical feature of fissure 7 is that in the Chimpanzee and Java ape-man by means of an arch-like fissure (6)‡ it joins the inferior precentral (5), and that in both this junction lies very near the inferior frontal-precentral junction, on the temporal perpendicular.

From these comparisons we see that what is usually called the inferior frontal of Chimpanzees is really the midfrontal, as rightly stated by CUNNINGHAM and CAMPBELL (*loc. cit. infra*), and that the real homologue of the inferior frontal, if present in this Chimpanzee, would be rather the steep archlike fissure, indicated as 4 ?, which, however,

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* Although it may not be excluded that a Hylobatid, attaining this size, might obtain an analogous development of fissures.

† As the frontal part of the temporal lobe is not complete in *Pithecanthropus* I took as its pole the outline indicated by McGREGOR in his 'Recent Studies on the Skull and Brain of Pithecanthropus' (1925).

‡ Fissure (6) is described by EBERSTALLER ('Das Stirnhirn', Graz, 1890) and CUNNINGHAM (*loc. cit.*) as the ram. horizontalis anterior of the inferior precentral.

even in this animal may acquire a more horizontal, humanlike arrangement (*cf.* CUNNINGHAM'S and CAMPBELL'S pictures). This also appears from the interesting relations with arterial supply discovered by SHELLSHEAR (1927*a*, 1927*b*, 1930).

If now we trace the development of the inferior 4 and midfrontal 7 in prehistoric, and recent, man we find the following :—

The rather small arch formed by 4 in *Pithecanthropus*, bending down into the orbital protrusion of the brain, is still present in a similar, though more widely arched, form, in the Rhodesian cast, but the inferior precentral 5 has shifted backwards in regard to the temporal perpendicular. A similar backward shift is also seen in the connection 6 of the midfrontal 7 with the inferior precentral 5.

In the Düsseldorf Neanderthal cast the 6 arch, connecting the midfrontal 7 with the inferior precentral 5, is also evident. As, however, the temporal pole is missing in this cast, we have no means of comparing the topography of these sulci with it.

Fortunately, however, the opercular protrusion in the Düsseldorf cast enables us to draw an additional (pointed) perpendicular on the lateral horizontal at the origin of the anterior Sylvian fissure 2.*

Drawing the same perpendicular in the Rhodesian cast it appears that in both the inferior precentral 5 runs closely along it. If, however, we draw the post-opercular perpendicular in *Pithecanthropus* the inferior precentral (5)† remains in front of it, for it does not lie as far behind the temporal perpendicular as it does in the two Neanderthal men. In the latter there may be two reasons for the more backward position of the inferior precentral in regard to the temporal perpendicular. Firstly, the temporal perpendicular may have shifted forward in Neanderthal man as compared to the Java ape-man, as a consequence of the temporal lobe having grown out further forward in Neanderthal man, and, secondly the precentral may have shifted backwards. As, however, the posterior border of the operculum has shifted backwards in Neanderthal man and nevertheless the inferior precentral corresponds with it, while in the Java ape-man it remains in front of it, this shows that not only the operculum in Neanderthal man has extended further backwards, but also the inferior precentral.

Both facts, the caudal shifting of the inferior precentral in regard to both perpendiculars, as well as the caudal displacement of the post-opercular perpendicular, show the increase of the inferior frontal lobe, which in man covers the frontal operculum. Both features, the more backward position of the post-opercular perpendicular and the more caudal position of 5, are evident also in the upper palæolithic Prdmost man, represented in the same figure, Plate 48.

Besides, these brains are higher than the lower paleolithic brains. Further developmental features observed in this race (*Homo sapiens fossilis*) are the tendency of the inferior frontal fissure to run more horizontally, or to make a frontal branch, as is especially evident in Prdmost IV and in the Vestonice (Winternitz) cast.

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* As far as I can see only one anterior Sylvian branch is distinct in my Neanderthal casts. In several upper palæolithic casts an ascending and horizontal anterior branch occur.

† Fissure 5A in *Pithecanthropus,* on top of 5, but somewhat more caudal, is the superior precentral.

Furthermore the occurrence of two anterior branches of the Sylvia, in addition to a fissura axialis operculi frontalis, which hitherto I had failed to find in any Neanderthal cast is very common in upper palæolithic casts.

The changes in the midfrontal region are still more conspicuous, especially in recent man. The uninterrupted course of the midfrontal fissure (7) in *Pithecanthropus* is also found in Rhodesian man and Neanderthal man (Düsseldorf and La Quina). In these casts it runs in a twofold curve from the inferior precentral* into the direction of the frontomarginal (9) with which it may connect, or nearly connect,† as it does in *Pithecanthropus*.

A marked feature of this sulcus, which may be derived from the horizontal branch of the arcuate fissure in monkeys, is, in recent man, its breaking up into several parts, usually arches, and losing its connection with the precentral; consequently the human midfrontal is often overlooked, and if it is complete it is sometimes taken for the superior frontal.

It is, however, an interesting fact that the uninterrupted condition of the midfrontal (7) and its continuity with the inferior precentral (5) by the arch (6) is so evident in some lower palæolithic casts, and that amongst recent human races this occurs more in dolichocephalic than in brachycephalic brains and especially in the dolichocephalic Negroes. This had already impressed SERGI (1909)‡, who gave an excellent account of the Herero brain.

I do not understand the statement made by POYNTER and KEEGAN (*loc. cit. infra*, p. 194) that in 75 per cent. of their hemispheres (13 brains) the midfrontal is represented by shallow irregular elements and that there is nothing to impress one with the importance attributed to this sulcus by EBERSTALLER.

Though interrupted in their figs. 1, 3 and 5 the fissure is extremely evident. In figs. 1 and 3 also, its connection (my 6) with the inferior precentral is clear. In their figs. 1 and 3 they probably labelled a part of this sulcus as superior frontal (although it connects with the fronto-marginal).

Fig. 3 shows five of SERGI's Herero hemispheres in which the classic, probably more original, relation of the midfrontal is extremely obvious, and in the two Soudanese brains preserved for me by Professor DERRY, Plate 42, this relation also occurs.

At the right-hand bottom is a picture borrowed from ELLIOT SMITH (1904), in which this sulcus, though interrupted, is quite obvious and in which the connection of the midfrontal (7) with the inferior precentral (5) by means of the arch 6 is still present in its classic form. In the Australian aboriginal brain the constancy of a distinct midfrontal appears from DUCKWORTH pictures and WOOLLARD'S paper (*loc. cit. infra*).

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[*] Only in the La Quina cast it is attached to the superior precentral, as already observed by ANTHONY (1913). Its ancient connection is, however, with the inferior precentral; this also occurs in apes, where both together may form the arcuate sulcus of simian anatomy.

[†] In WERNICKE'S fronto-marginal we distinguish a transverse part (running parallel to the edge of the brain) and an ascending branch, standing nearly perpendicular on the former. This ascending branch usually is the most evident part of the sulcus and it is to this branch (9) that I refer.

[‡] *See* especially his brains I, II, III, V and X, and also BIANCHI (1922).

[§] The phylogenetic relation of arch (6) with the simian arcuate is rightly indicated by ELLIOT SMITH.

It also occurred in FLASHMAN'S Australians and in the only Australian brain in my collection. Another feature of the Negro brain, the lower (more lateral) position of the superior frontal (POYNTER and KEEGAN) seems also to be reflected in the lower position of the midfrontal. Perhaps this is due to a lesser development of the middle region of the frontal lobe, a possibility also alluded to by the forenamed authors. Naturally the question arises whether the less frequent interruption of the midfrontal, and especially of its connection with the inferior precentral in the latter race, may be interpreted as a symptom of a lower organisation in this part of the brain.

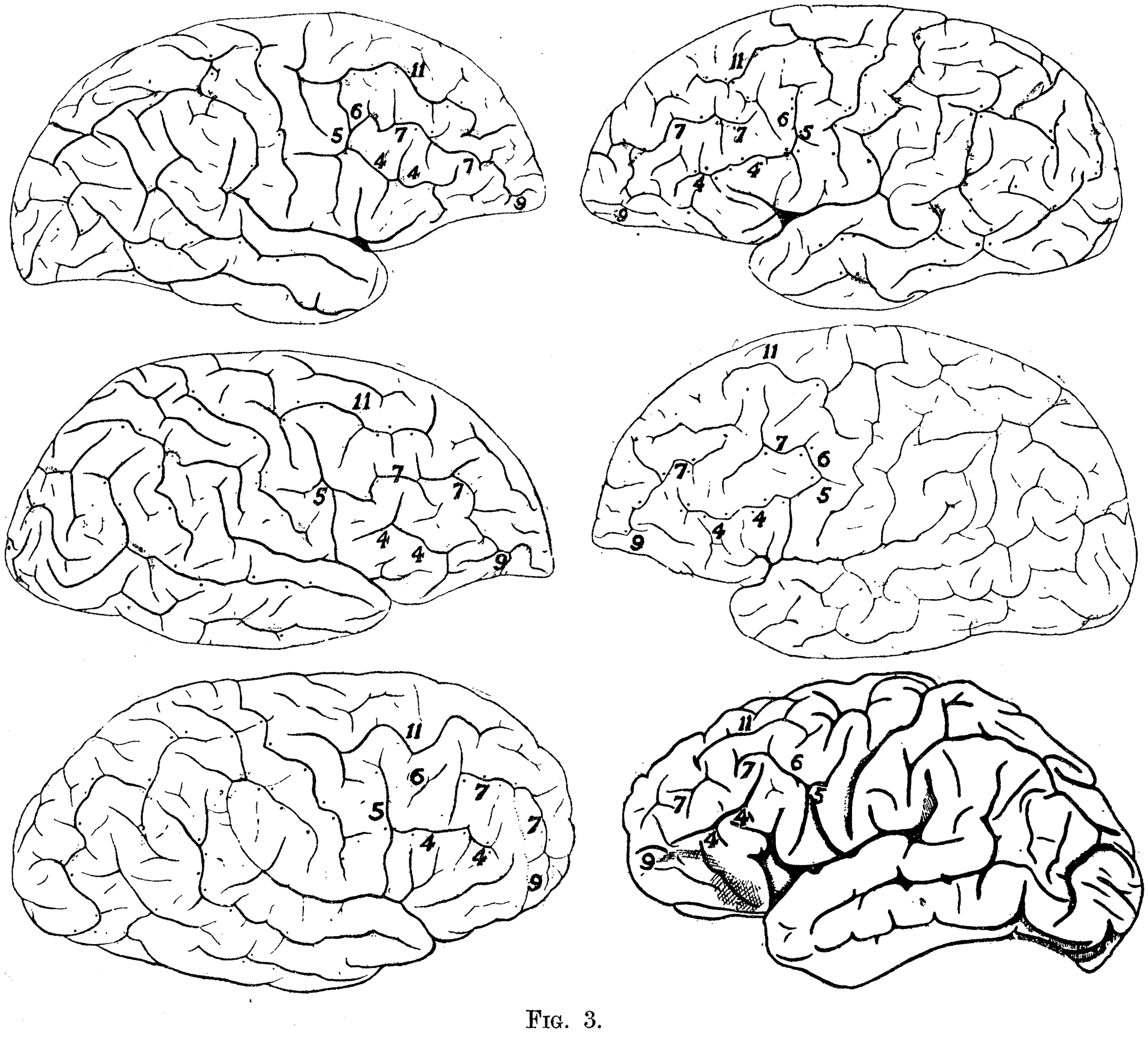

FIG. 3.

Although some of the facts mentioned may induce us to accept a simpler organisation of the Negro brain we should be careful in basing this chiefly on the midfrontal fissural relations, since this condition is also found in European longheads, although perhaps less frequently.

The same holds good for the long prelunate sulcus mentioned by POYNTER and KEEGAN for the Negro brains, but occurring also in the pictures of dolichocephalic Dutch brains described by WANG HWEI WEN and myself* and in the second brain of Plate 38 (P.P. = prelunate). This often coincides with a flattening of the lunate crescent.

If a continuous midfrontal, connecting with the inferior precentral is less frequent with Europeans we should realize the fact that such an exquisite dolichocephaly as with Negro races is rare in Europe. Still we may consider it as a more primitive arrangement, as the continuous midfrontal, including its connection with the precentral, seems to have predominated in the Neanderthal race as it does in *Pithecanthropus*, and apes.

The survival of this more primitive arrangement in some races may, however, be due to the fact that just as in primitive man the skull form is a rather long one, which seems to favour this condition as it favours the simpler course of the Sylvian and temporal sulci.

In meso- and brachy-hypsicephalic both conditions are less frequent, although the simpler midfrontal also occurs with such races.†

But on the other hand the tendency of the midfrontal sulcus to split up into pieces, and to lose its connection with the precentral in general, may have to do with the evolution of the frontal lobe as appears from the fact that this sulcus and its homologue, the horizontal branch of the arcuate, are so constant even in brachycephalic apes.

To explain from an evolutionary viewpoint the fragmentation of this sulcus in most recent races we have to consider the cytotectonic and physiological development of this lobe.

The gradual more caudal extension of the lower part of the frontal area in monkeys, apes and man, as evidenced by the caudal displacement of the inferior frontal and orbital operculum, is confirmed by the cytotectonic researches of all who worked in this field (CAMPBELL, BRODMANN, MOTT, the VOGTS and their school).

If we admit that the value of the inferior precentral as a limiting sulcus of the frontal area holds good also for *Pithecanthropus* and Neanderthal man, we may suppose that the backward extension of the frontal area as indicated by the inferior precentral in *Pithecanthropus* was about the same as in the Chimpanzee ; in Neanderthal man it was greater, and still greater in the Prdmost race, in the three last mentioned races also gradually extending more into the orbital operculum. This chiefly concerns the lower frontal convolutions.

For our knowledge of the midfrontal area in anthropoids the most important work is that of CAMPBELL (1905, 1916), who, in his "Localisation of Cerebral Function," described the relations in a Chimpanzee and Orang-Utan and later added a description of the relations in the Gorilla.

In CAMPBELL'S researches it is fortunate that the relations in the three anthropoid apes and in man are examined by one author, who consequently applied the same

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* WANG HWEI WEN and ARIËNS KAPPERS (1924).

† So for the Chinese, *see* Dr. VAN BORK'S work, fig. 23 and p. 40, and also SCHUSTER'S description of three Chinese brains ('J. Anat. Physiol.,' vols. 42 and 43).

cyto- and myelo-tectonic criteria to his slides of all these specimens. Moreover, CAMPBELL gave more attention to fissuration than many students in this field, who were too much convinced of the futility of fissural studies.

It is interesting to note that CAMPBELL is one of the few neurologists who describes the usually called inferior frontal of the Chimpanzee as the intermediate frontal (= midfrontal). Besides, underneath this fissure in his Gorilla he (and CUNNINGHAM) identified a small and, in his Chimpanzee a larger, frontal offshoot of the inferior precentral as homologous to the human sulc. frontalis secundus = s. frontalis inferior (*loc. cit.* 1905, p. 216). He found it to be more or less the dorsal boundary of an area which he distinguishes from the other part of the frontal lobe, in the same way as he did in man.*

Although his identification of the cytotectonic field underneath the inferior frontal with the intermediate precentral area is questioned by BRODMANN and MAUSS, for our purpose it suffices that both he and BRODMANN recognised this area in man as being different from the rest of the frontal lobe.

In my opinion CAMPBELL'S interpretation of the frontal fissures in anthropoids and their homologies with the human fissuration is right.

The fact that in recent human races the midfrontal sulcus is so frequently broken into pieces and its connection with the precentral interrupted, indicates that the region through which the midfrontal runs is a region of great developmental changes. The fissural changes occur especially in fields 8 and 9 of BRODMANN. Concerning the function of field 8 in man, we know, PREVOST (1868), SAHLI (1906), FÖRSTER (1923), FÖRSTER and PENFIELD (1930), that it contains the centre for the conjugate deviation of the eyes (field 8α, β, and γ).

On account of experiments with dogs (and monkeys) in which similar reactions occur, in stimulating an analogous (precrucial) region (field 12 in dogs) FERRIER (1877, 1887) had already concluded that the prefrontal lobe is *par excellence* a centre of attention. For dogs and monkeys it was confirmed by BIANCHI (1922), in lemurs by MOTT and VOGT, in monkeys by BEEVOR, HORSLEY and SCHÄFER and VOGT, and in apes by SHERRINGTON and his collaborators GRÜNBAUM and LEYTON (1901, 1917).

It is interesting that the area containing this field in all these animals is exactly the area surrounding the connection of the midfrontal with the precentral (*cf.* for apes, SHERRINGTON (1901 and 1923, fig. 10) for *Ateles* and *Semnopithecus* VOGT (1907) and for man FÖRSTER and PENFIELD).

From area 9, fronto-pontine fibres arise (v. MONAKOW, 1905, 1914) and perhaps cerebello-rubro-frontal impulses arrive here.

It would not be strange if the gradual increase in importance of the centre of conjugate deviation in field 8 of BRODMANN, and pragmatic functions connected with cerebellar

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* Although he added this inferior frontal field to his intermediate precentral area (= the precentral agranular area of BRODMANN and MAUSS), BRODMANN agrees with him so far as he also distinguishes it from the ordinary frontal field and calls it the subregio frontalis inferior in man. He did not indicate it in this Chimpanzee, nor did MAUSS in his Orang-Utan.

projections (in field 9 of BRODMANN) should result in breaking up the fissural arrangement, originally so simple, in this part of the frontal lobe.

That an extension of function involves a breaking up of a fissural pattern originally simple, is best demonstrated by the cerebellum itself, in which the parallel position of sulci, originally so regular, is changed to a very irregular cauliflower-like arrangement in those animals where the cerebellar mechanism is more complicated, as, *e.g.*, appears from a comparison of the ansate lobe of the cerebellum in the whale and the elephant.

This much is sure that the distinction of the present human brain not only consists in a more marked development of the inferior frontal region (the speech centres) but also of the midfrontal region of which the strong development may also find an expression in the fact stated by QUANJER (1912) that the midfrontal convolution is never opercularised by the inferior frontal convolution, while the opposite occasionally occurs.

The fact that both the inferior as well as the midfrontal convolutions increase in man compared to monkeys and apes explains another feature of the human midfrontal, viz., its more dorsal location* that causes, more frequently than in anthropoids, parts of it to be taken for, or even be superposed upon, the superior frontal (*cf. also* SERGI's excellent work on this subject: 1913, 1926).

It is clear that the tendency of the short but usually quite regular inferior temporal sulcus of anthropoids to break up in man in various pieces (either transverse or longitudinal fissurets) must also be explained along the same lines. WOOLLARD (*loc. cit.* II) showed that the acoustic cortex, especially the relation between the depth of the supra- and infra-granular layers is less developed in the Australian aboriginal brain, a fact that fits in very well with the findings of VAN NOORT (1917) in the Madurese and with the fact that this cytotectonic field is late in phylogeny to acquire its typical characteristics (BRODMANN). As in the second temporal convolution, the temporo-pontine fibres arise; pragmatic functions may also act a part here as they do in field 9 of the frontal region. ELLIOT SMITH (1927) has also pointed to the evolutionary importance of the temporal region in connection with pragmatic functions.

In this breaking up of sulci we have the opposite of the confluence of sulci in becoming adapted to cytotectonic and functional fields, so evident in the Rolandic which, represented by the coronal and ansate of carnivores, is usually still indicated, even in lemurs, by two fissurets, but in all monkeys is a homogeneous fissure. Similarly the calloso-marginal is still represented in the former by two fissures, the genual and the intercalary fissure, and finally the calcarine arising from the retrosplenial and its processus acuminis in Ungulates and Carnivora.

Adaptation of fissures to functional areas also described by ELLIOT SMITH either as limiting sulci (*e.g.* Rolandic and rhinal) or as axial grooves (calcarine, hippocampal) chiefly occurs in such fields as phylogenetically become more and more stabilised and ripen early in ontogeny.

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* The lower course of the sulcus in anthropoids evidently induced so many anatomists to mistake it for the inferior frontal.

Fragmentation of sulci, however, prevails in recently expanded fields, or on the borderline of such fields, as we see with the midfrontal. Another example is the lunate; represented already in Carnivores by the postlateral it is very distinct in the larger Prosimiæ (*e.g.*, *Indris* and *Lemur varius*) Simæ and Anthropoids.

The lunate occurs also on the right occipital lobe of *Pithecanthropus*, where it still lies in front of or on the lambdoid suture as in apes. Moreover it occurs in extinct human races (in the Düsseldorf cast behind this suture). It is frequently observed in recent man, usually (but not always, *see above*) behind the lambdoid suture, showing all its satellite fissures (prelunate, the ypsiliformis, inferior occipital), as we know from the classic work of ELLIOT SMITH. But more often in man it is only represented by little bits and not rarely it is broken up by the evolutionary changes in the visuo-psychic area.

I end with the apology that whereas the first FERRIER LECTURER dealt with the most intricate physiological relations of the central nervous system I have dealt with such an old morphological subject.

We should, however, not lose interest in the problem of fissuration, especially as it has been illuminated by the work of physiologists and histologists, and found new applications for palæontologists and anthropologists.

Studying it from an anthropological viewpoint we should keep in mind that mechanical as well as functional correlations influence the surface anatomy of the human hemispheres.

DESCRIPTION OF PLATES.

PLATE 36.—A, brain of *Canis* fam. (Dutch shepherd dog); B, of *Ursus malayanus*; C, of *Ursus maritimus*; D, opened insula of *Ursus malayanus*.

PLATE 37.—A, the brain of a 7 months fœtus; B and C, new-born brains; D, the brain of a child of 1 month; E, of 12 months.

In fig. B the lateral and mesial photographs are not of the same brain.

PLATE 38.—Dolichocephalic Dutch brains. (The brain *in situ* is English.) P. . . P = prelunate sulcus.

PLATE 39.—Brachycephalic Dutch brains.

PLATE 40.—A, B, C, D, Armenian brains, and E, a Lebanese brain. The fissure in front of 1 is the lunate sulcus.

PLATE 41.—Two brains of Egyptians (top: female brain, skull index 72·2; two lower figures: male brain, skull index 78).

PLATE 42.—Two Soudanese brains (top: male, skull index not registered, but apparently dolichocephalic; two lower figures: female, skull index 77·61). Note the well-developed rostrum in the left-hand top and bottom figure and the high insertion of the posterior calcarine, more frequent with brachycephalics.

PLATE 43—Brains of Northern Mongols (left by V. STEFKO, right by G. RETZIUS).

PLATE 44.—Chinese brains. Brain index A = 83·7; B = 80·1; C = 77·7. The cephalic indices are about 1·5 to 2 lower.

PLATE 45.—Brains of Japanese from Sendai (North Japan).

PLATE 46.—926 and 938, brain of a female and male Toba Batak, 931 and 934 brain of a female and male Karo Batak.

PLATE 47.—A, Bathrocephalic Dutch skull; B, Bathrocephalic Batak brain; C and D, skull and brain of a deformed Toulousaine head (after Ambialet); E and F, skull and brain of a form artificially deformed frontally strongly sloping head (after Ambialet). R. . . R = Rolandic fissure. The deep dimple between 7 and 4 is my 8.

PLATE 48.—Right from top, brain of an Orang-Utan and a Chimpanzee, left hemispheres reversed for easier comparison, with the right hemisphere of *Pithecanthropus erectus* (DUBOIS).

Left from the top, endocranial casts of the man of Rhodesia, Düsseldorf and Prdmost III.

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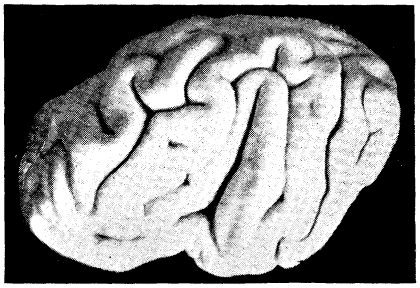

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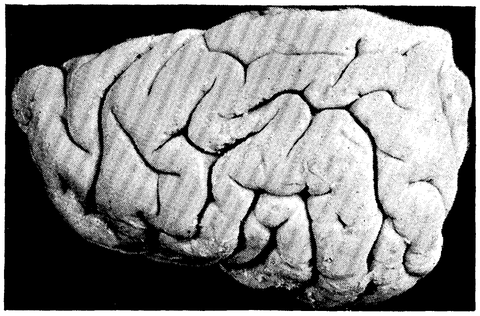

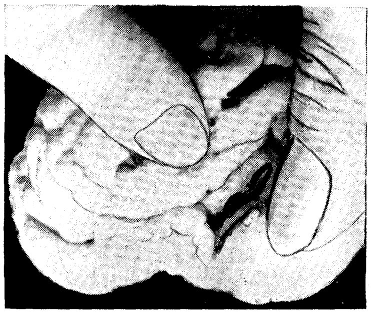

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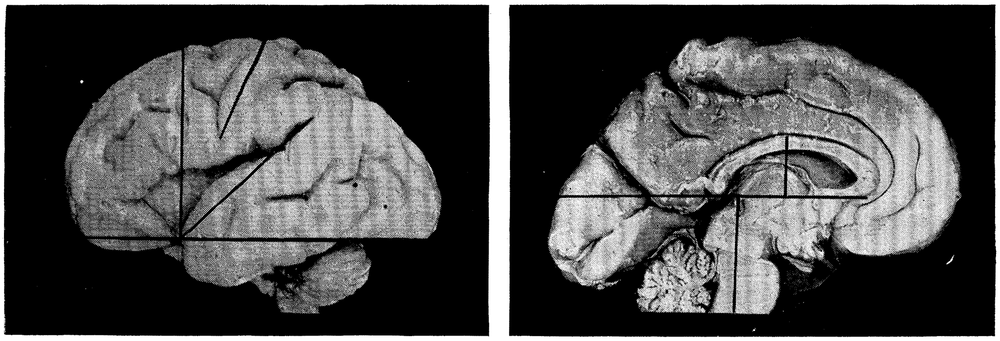

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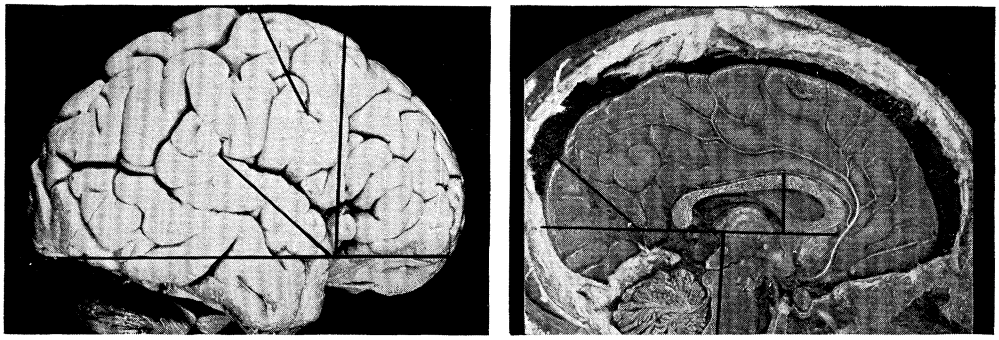

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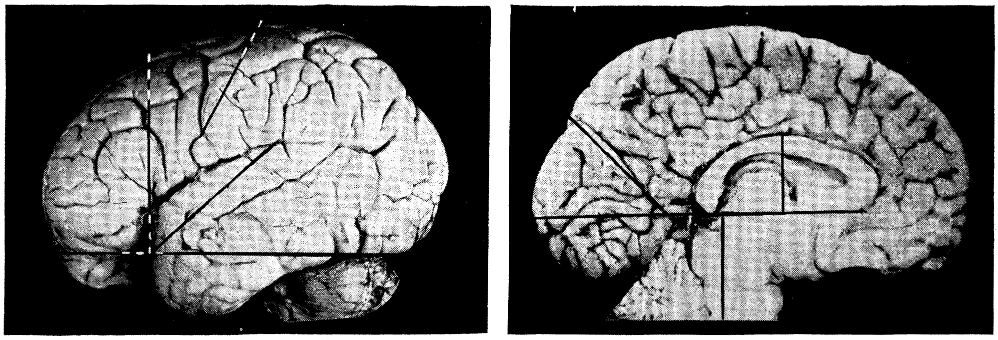

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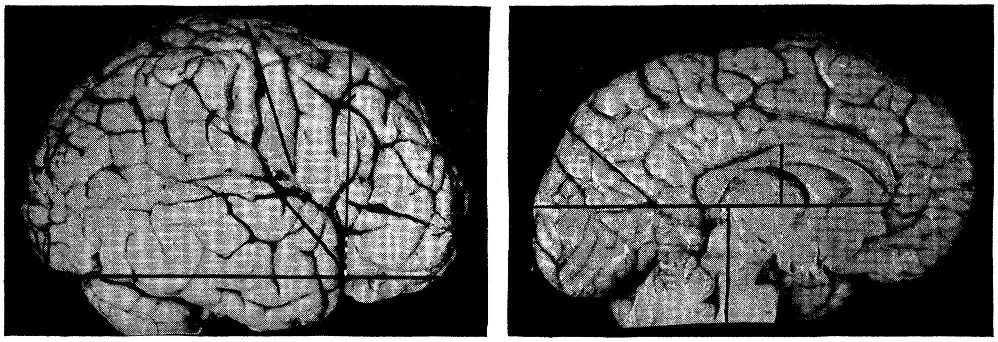

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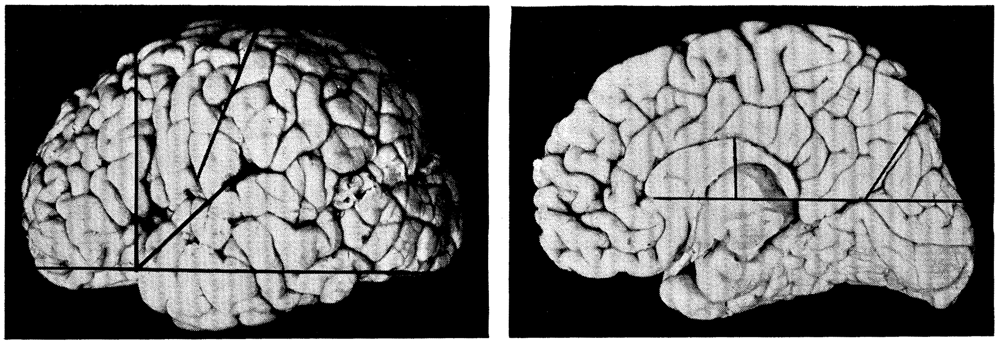

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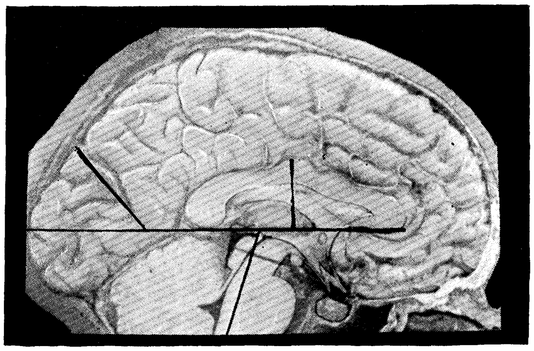

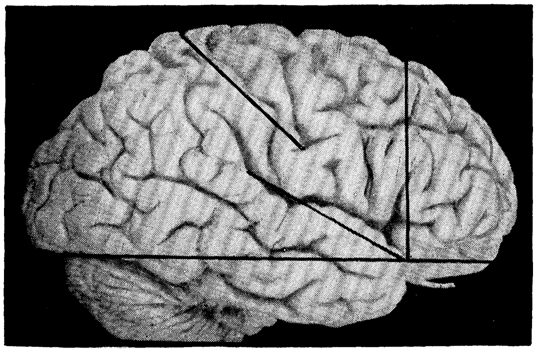

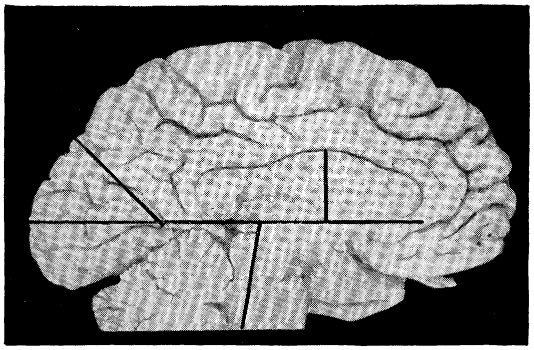

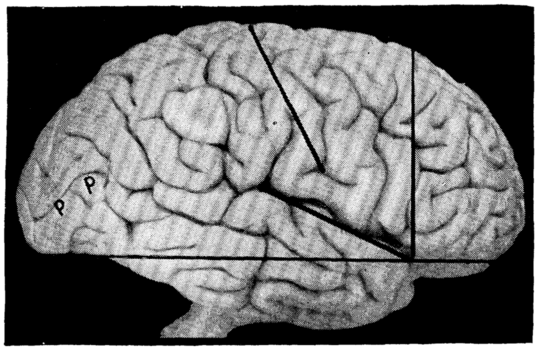
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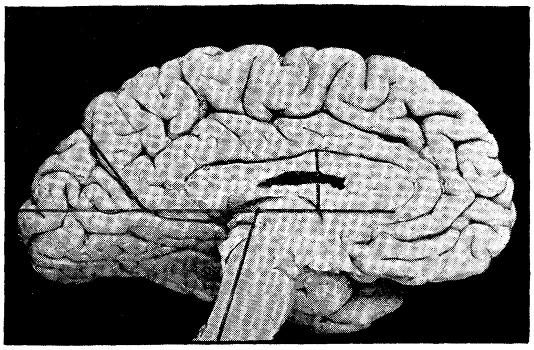

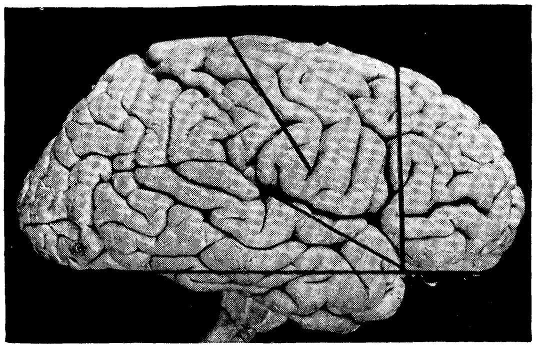

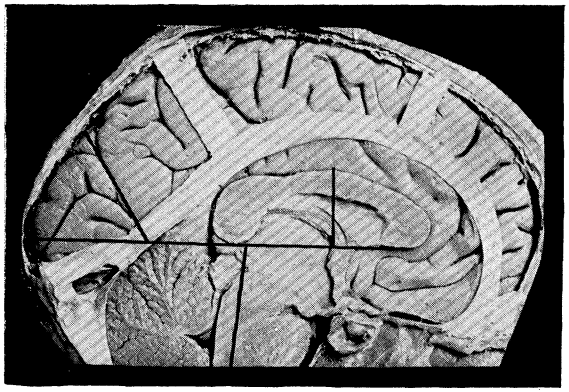

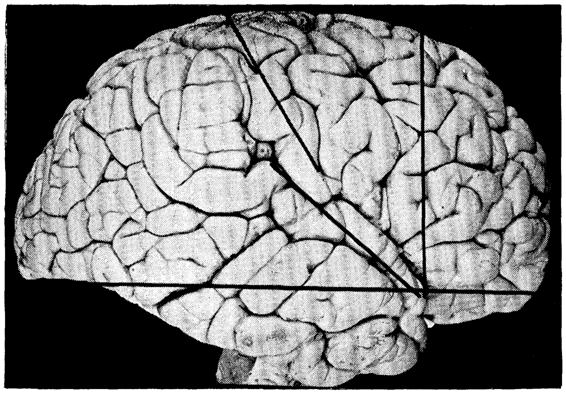

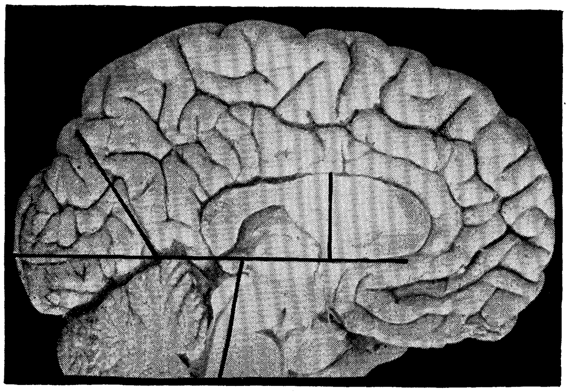

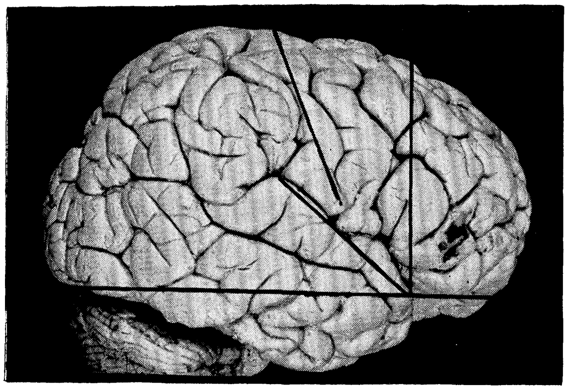

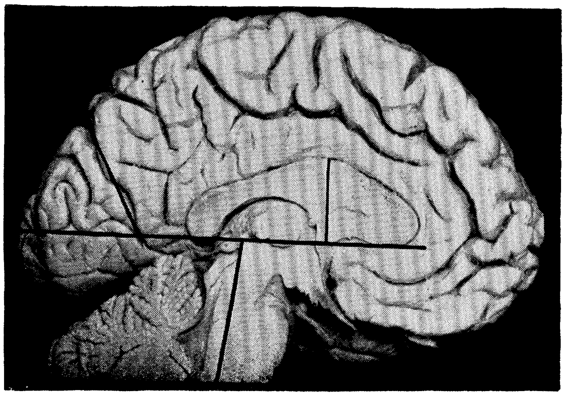

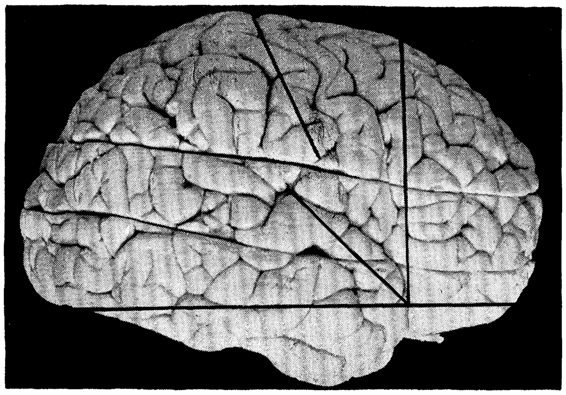

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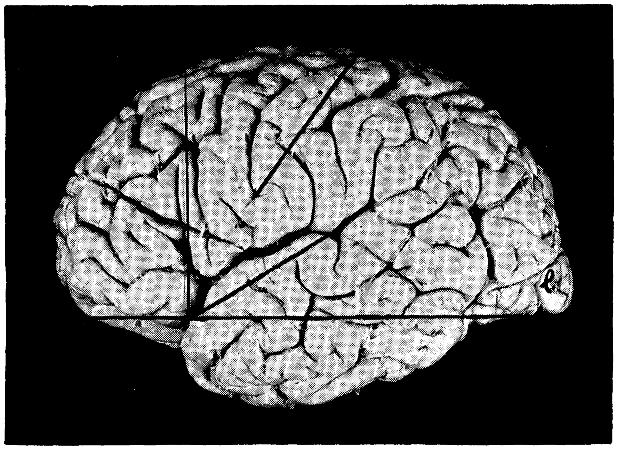

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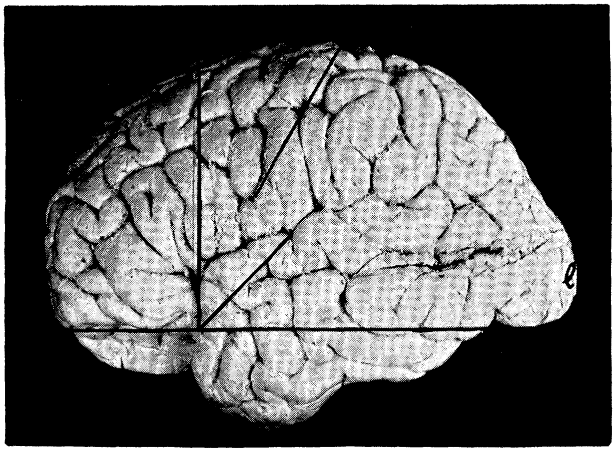

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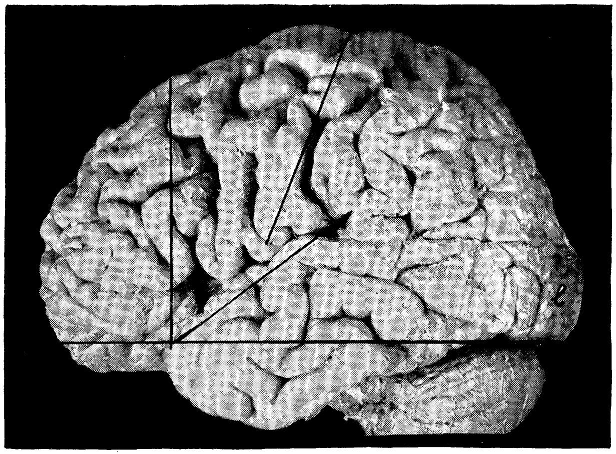

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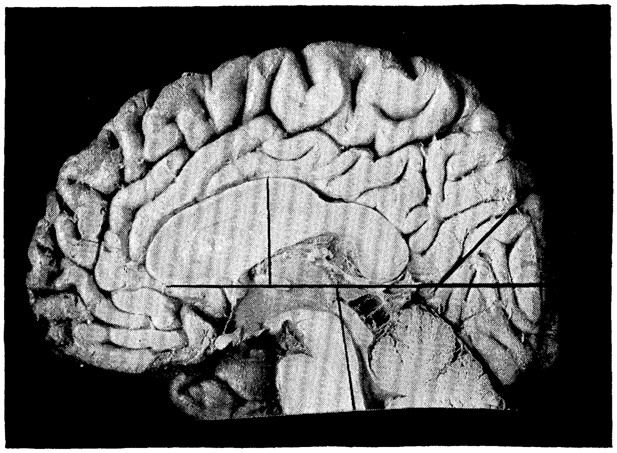

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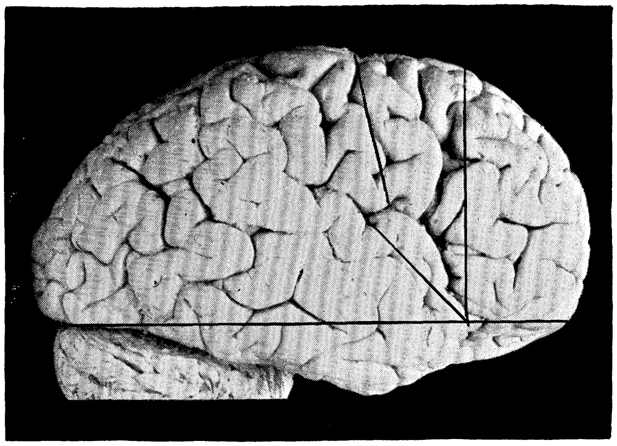

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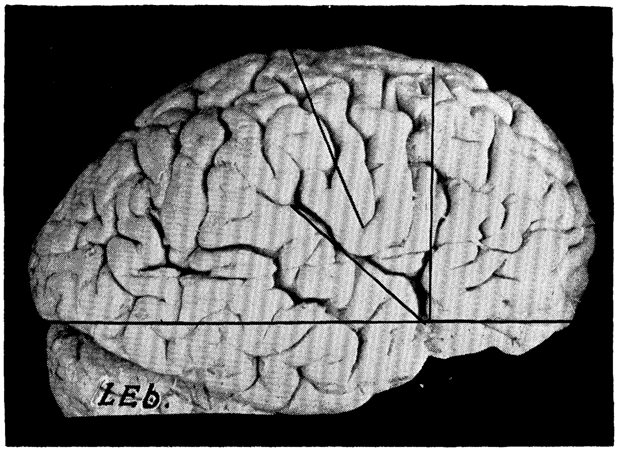

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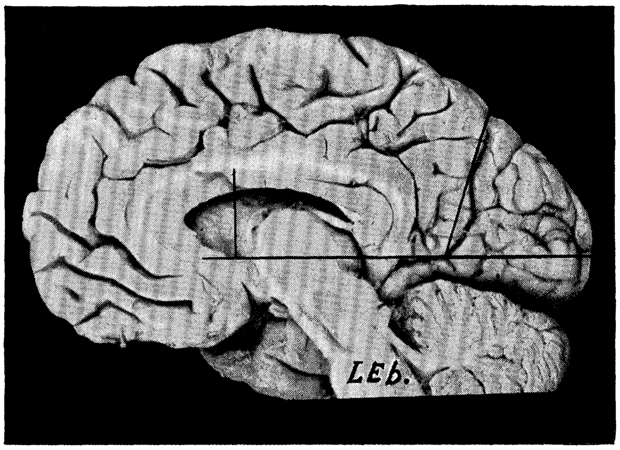

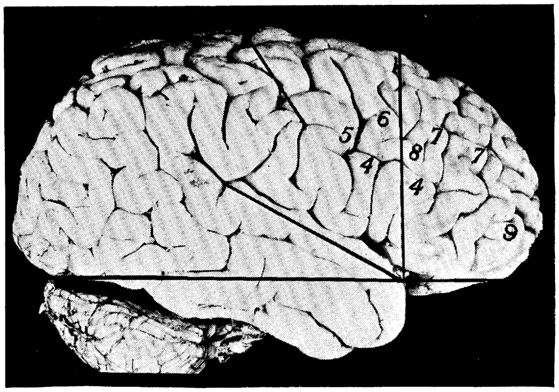
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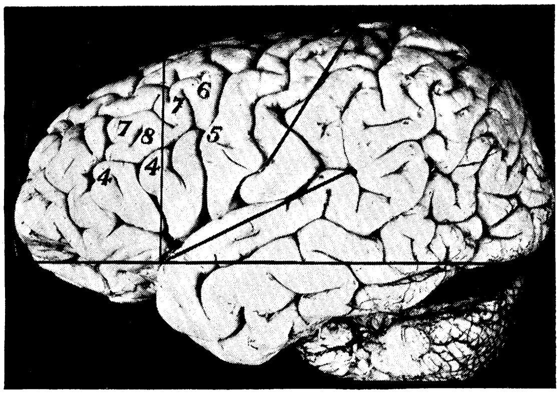
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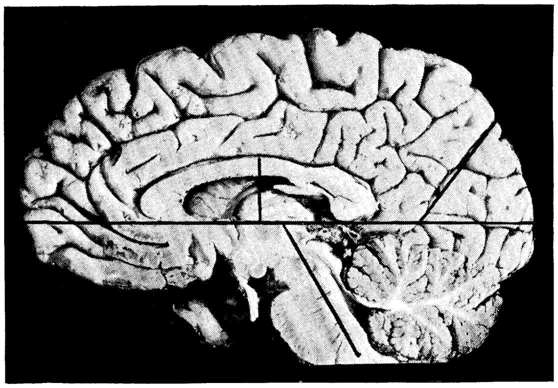

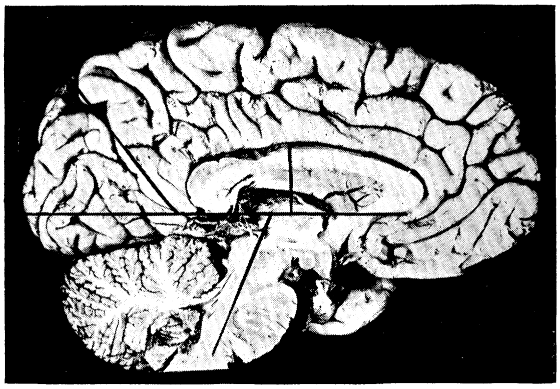

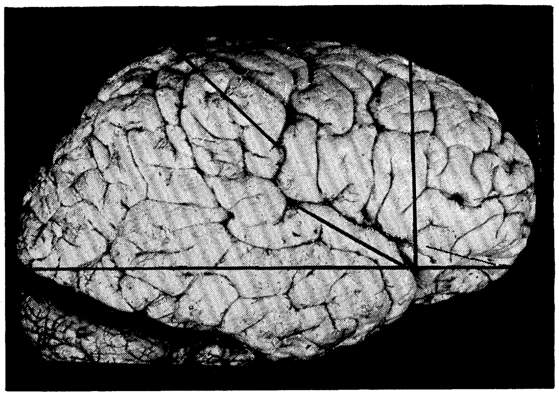

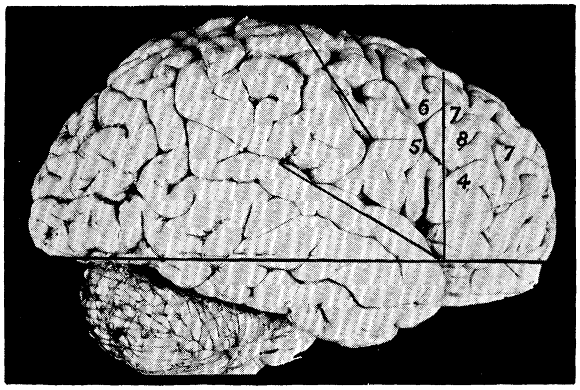
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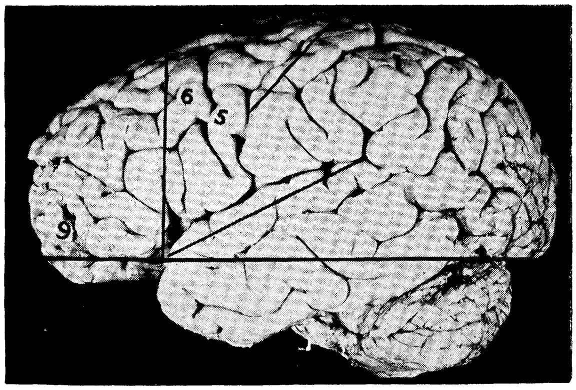
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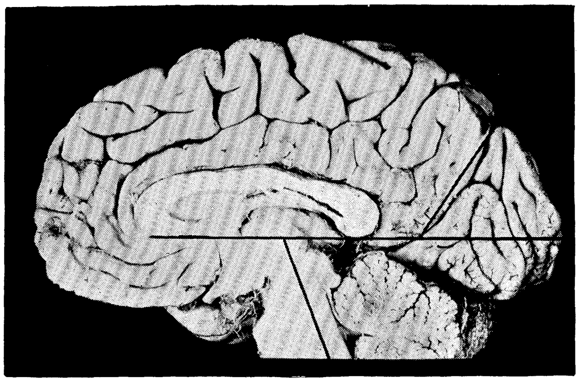

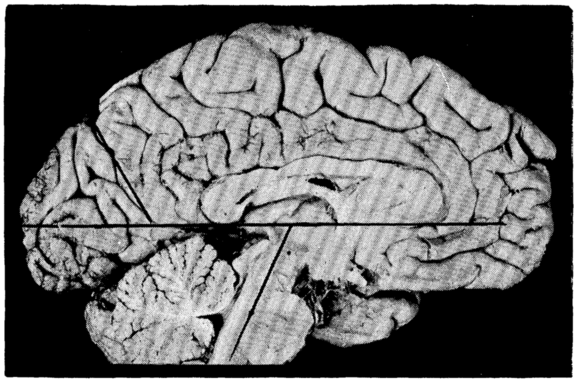

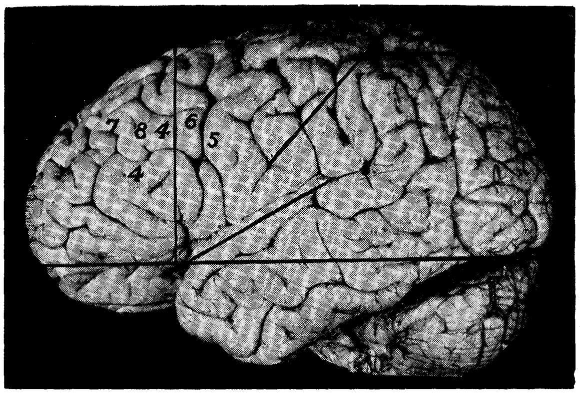
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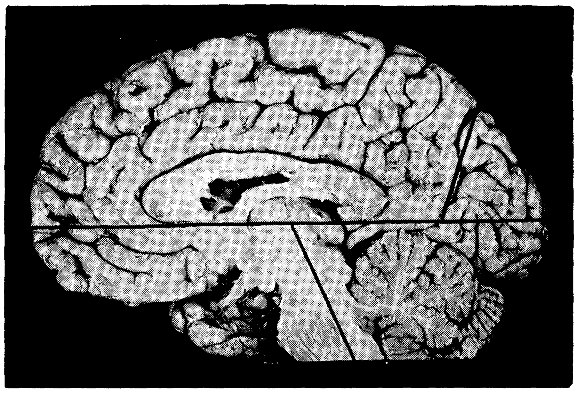

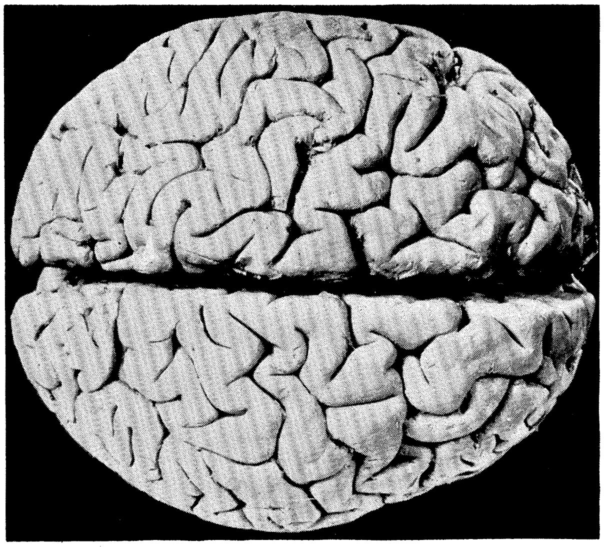

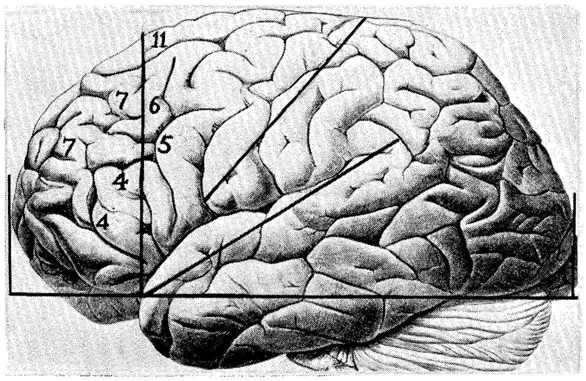
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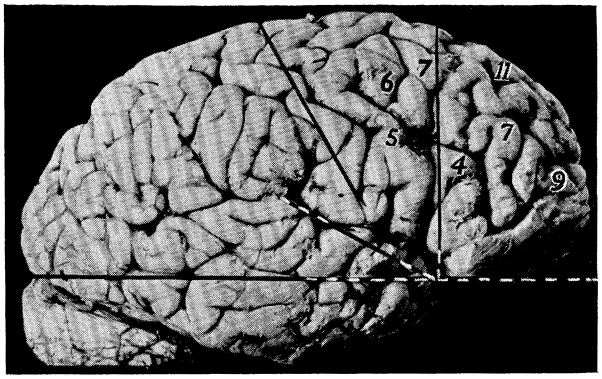
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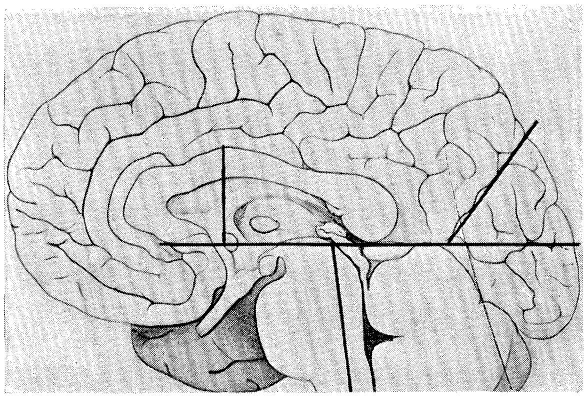

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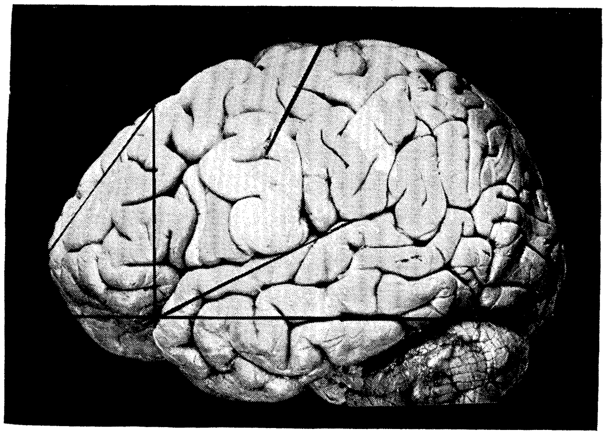

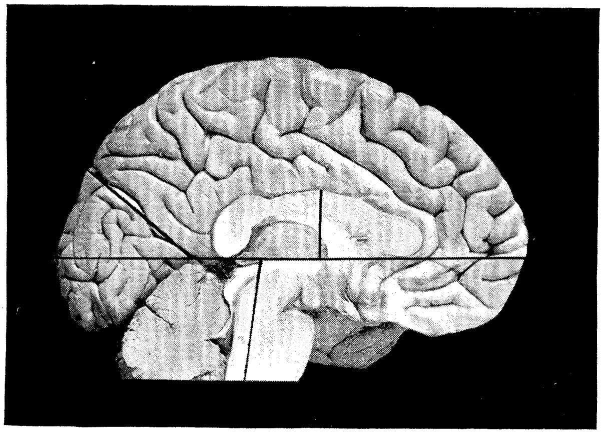

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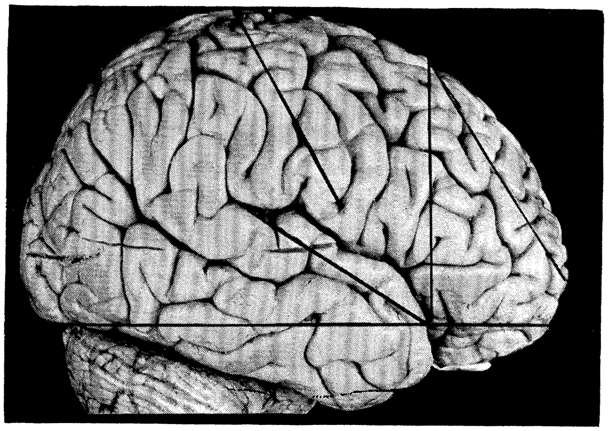

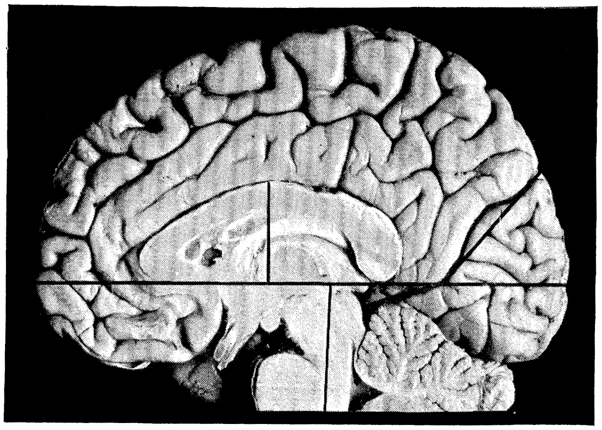

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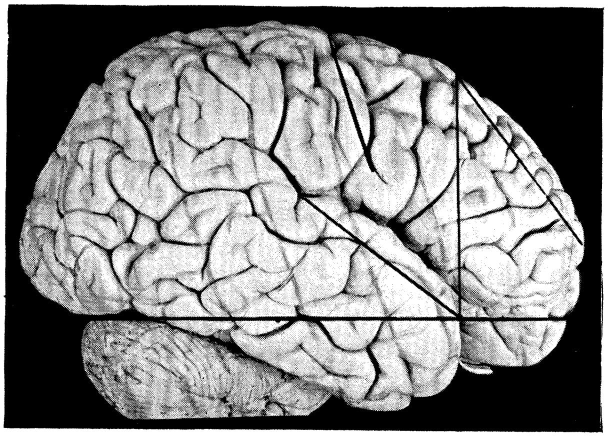

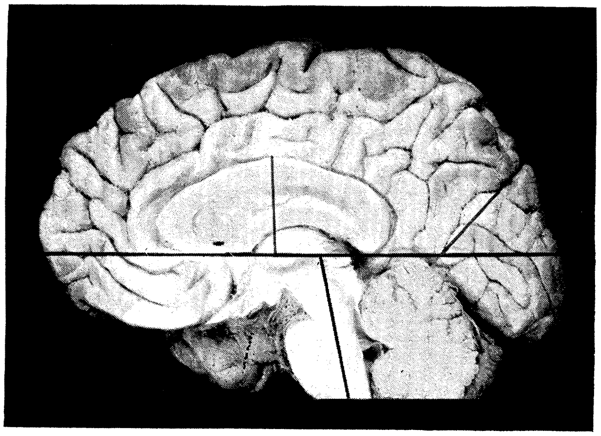

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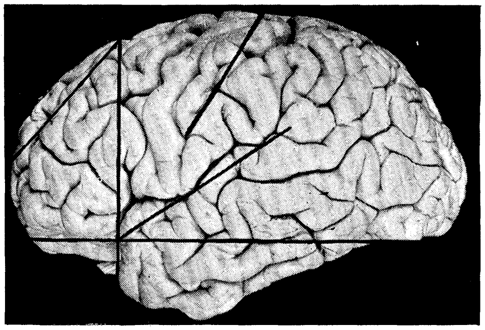

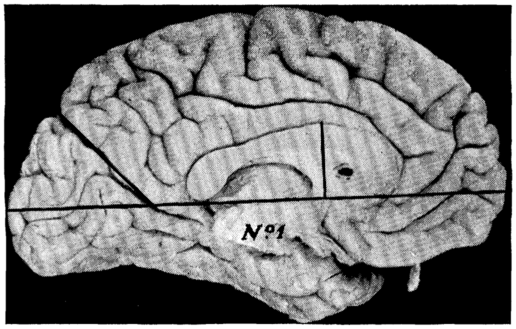
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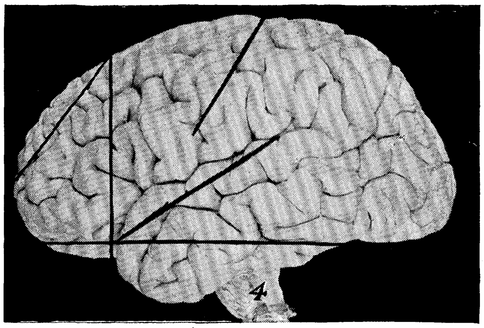
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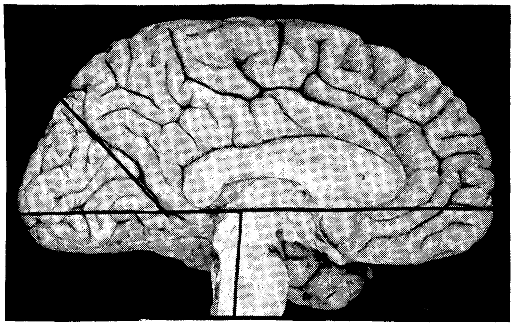

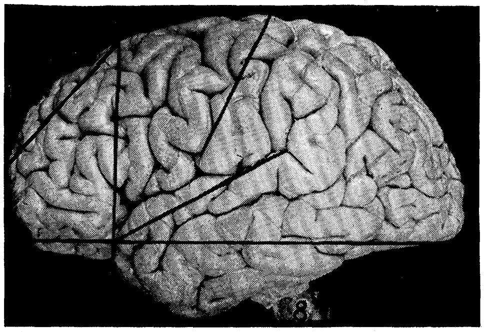
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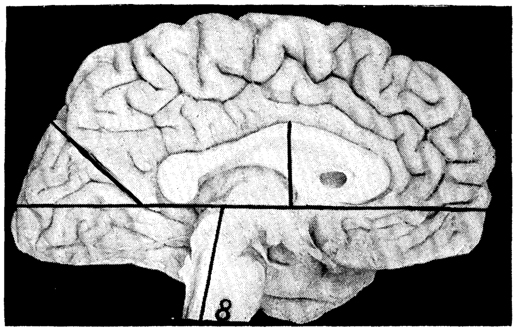
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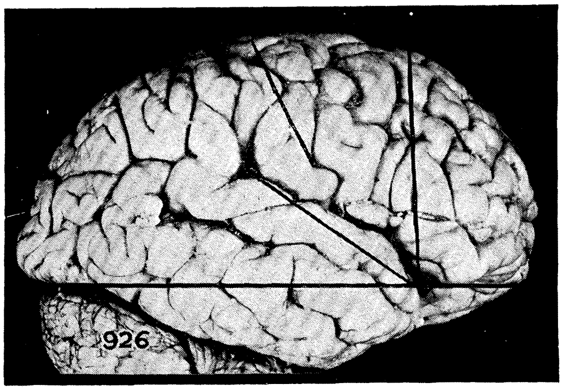
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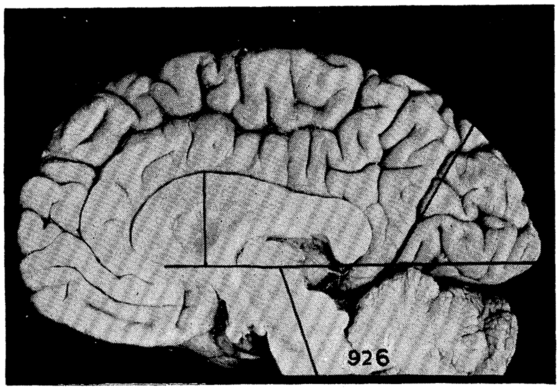
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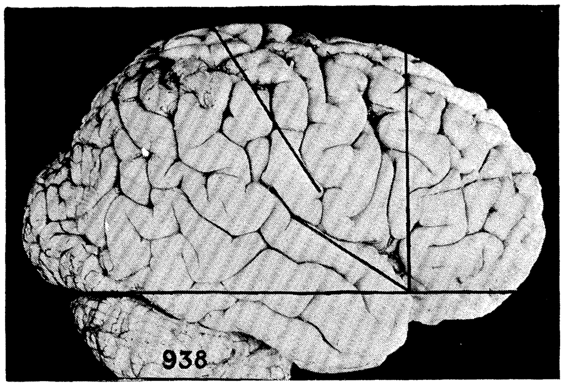
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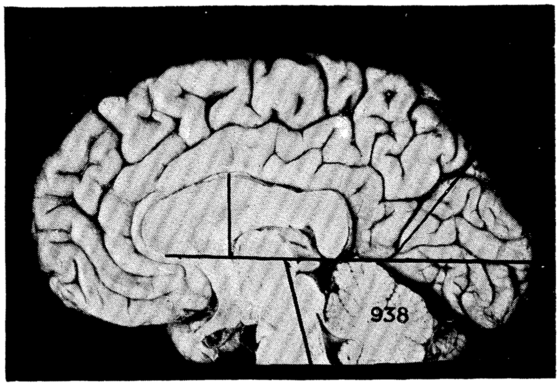
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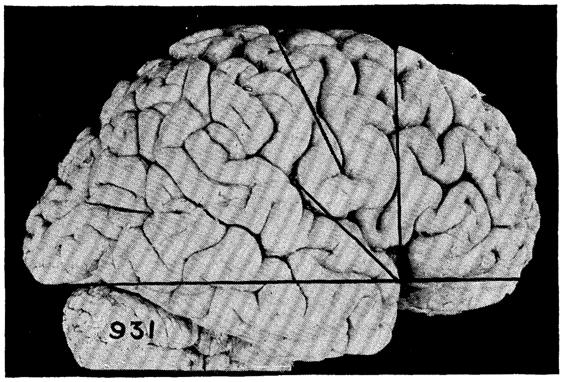
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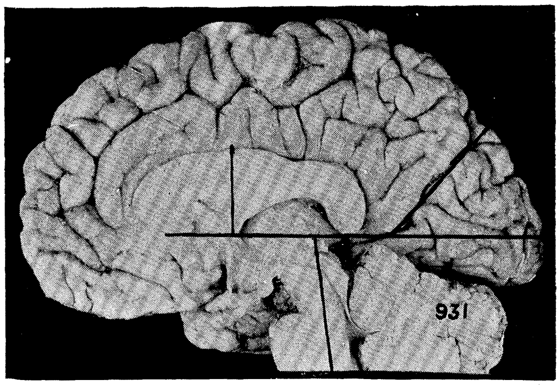
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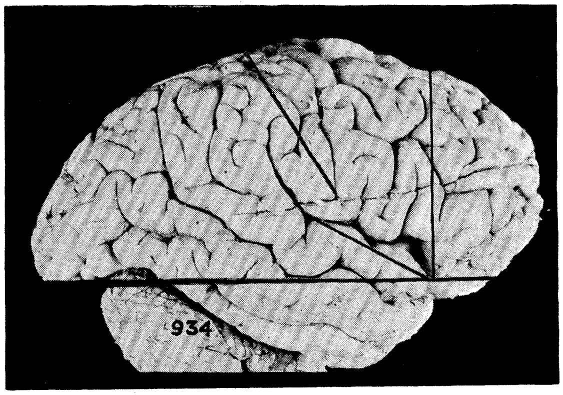
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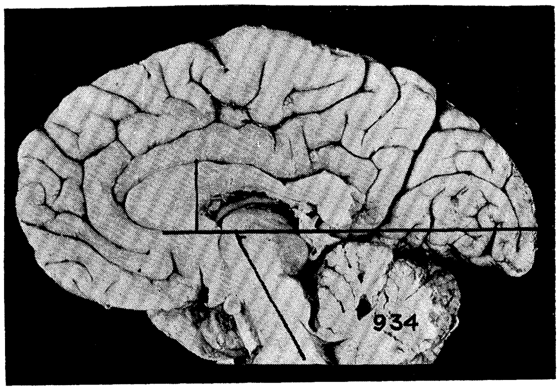
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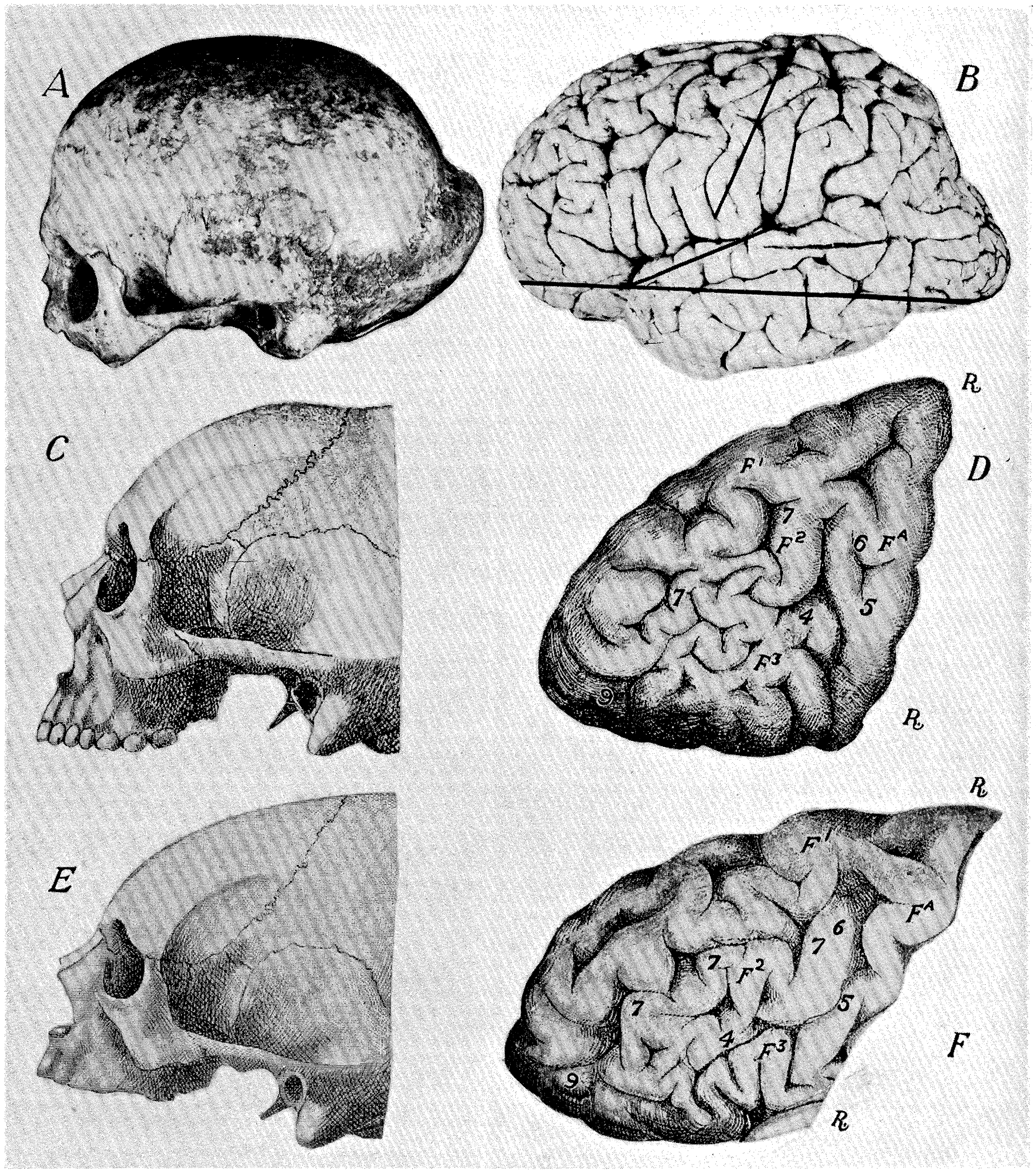
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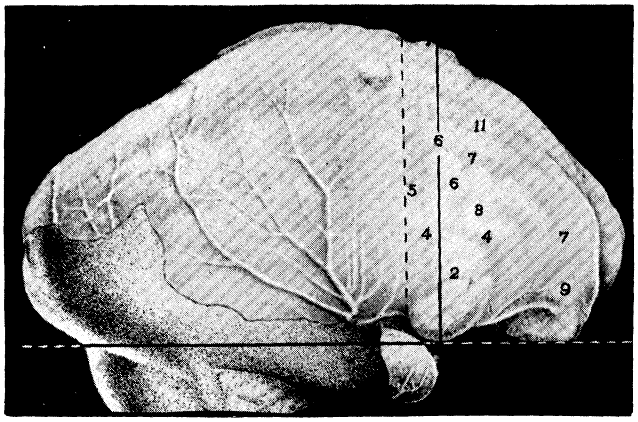
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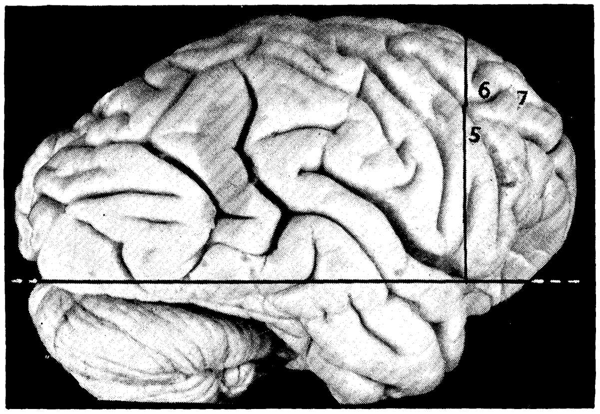
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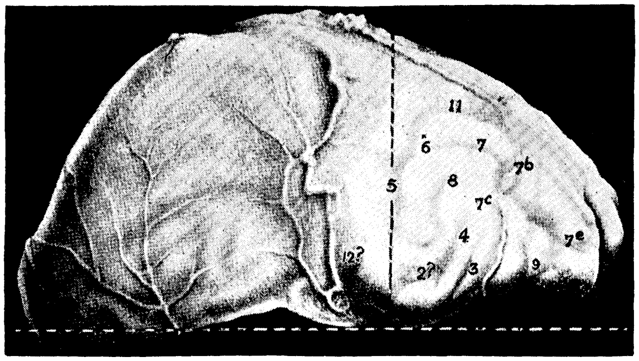
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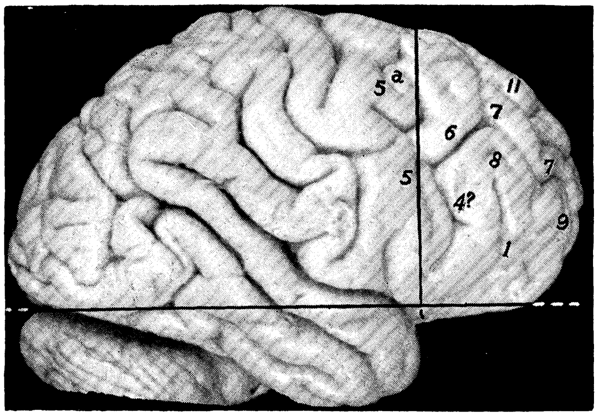
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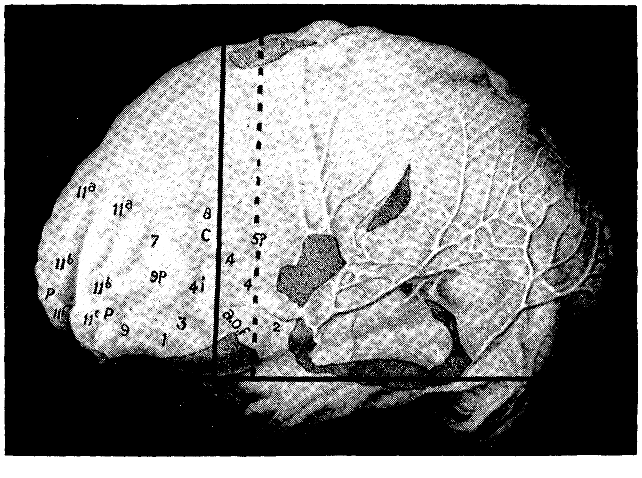
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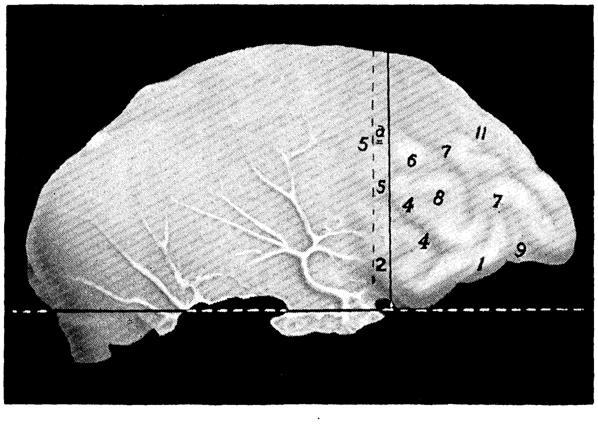
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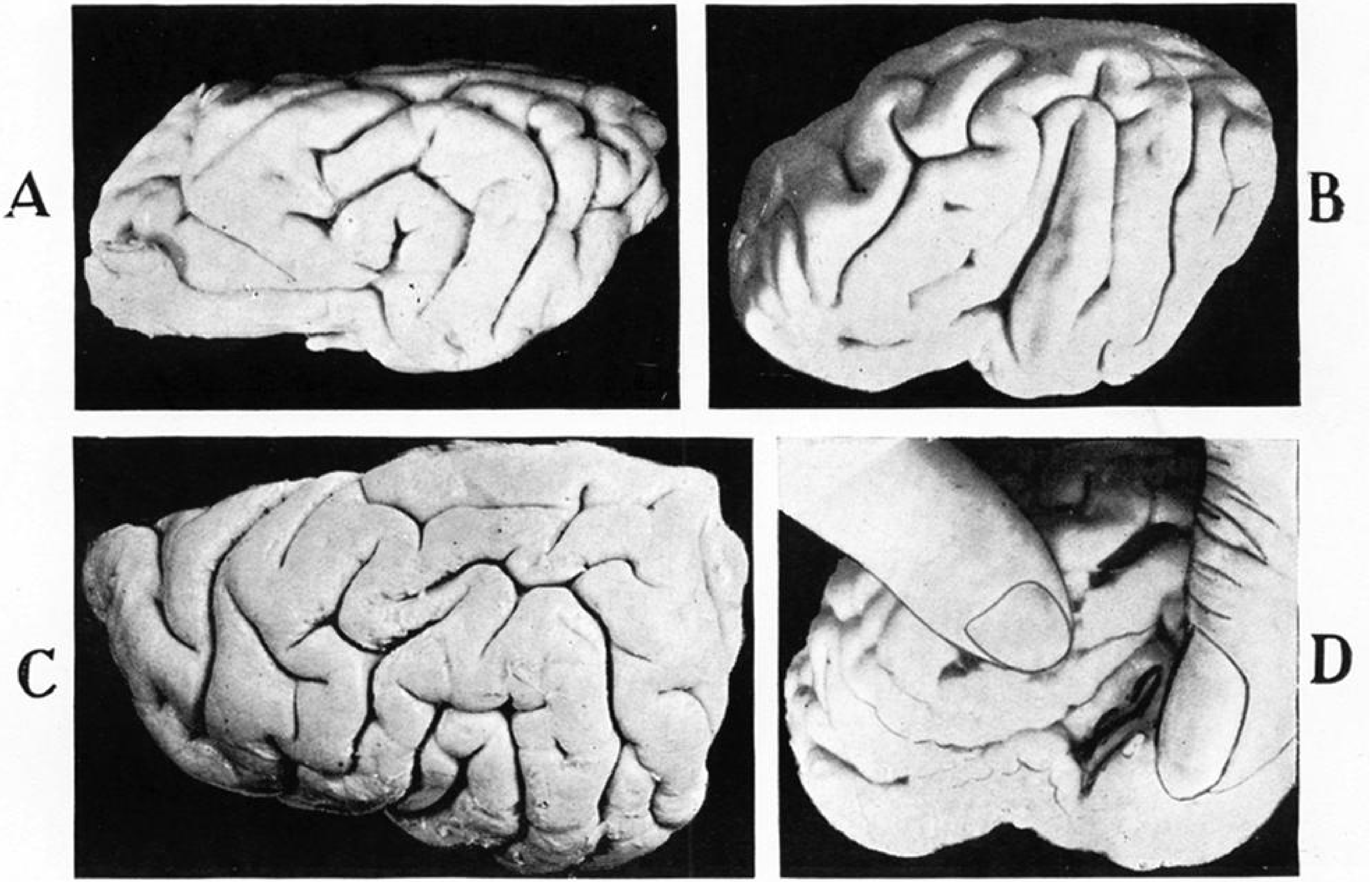

PLATE 36.—A, brain of *Canis* fam. (Dutch shepherd dog) ; B, of *Ursus malayanus* ; C, of *Ursus mariti*
D, opened insula of *Ursus malayanus*.

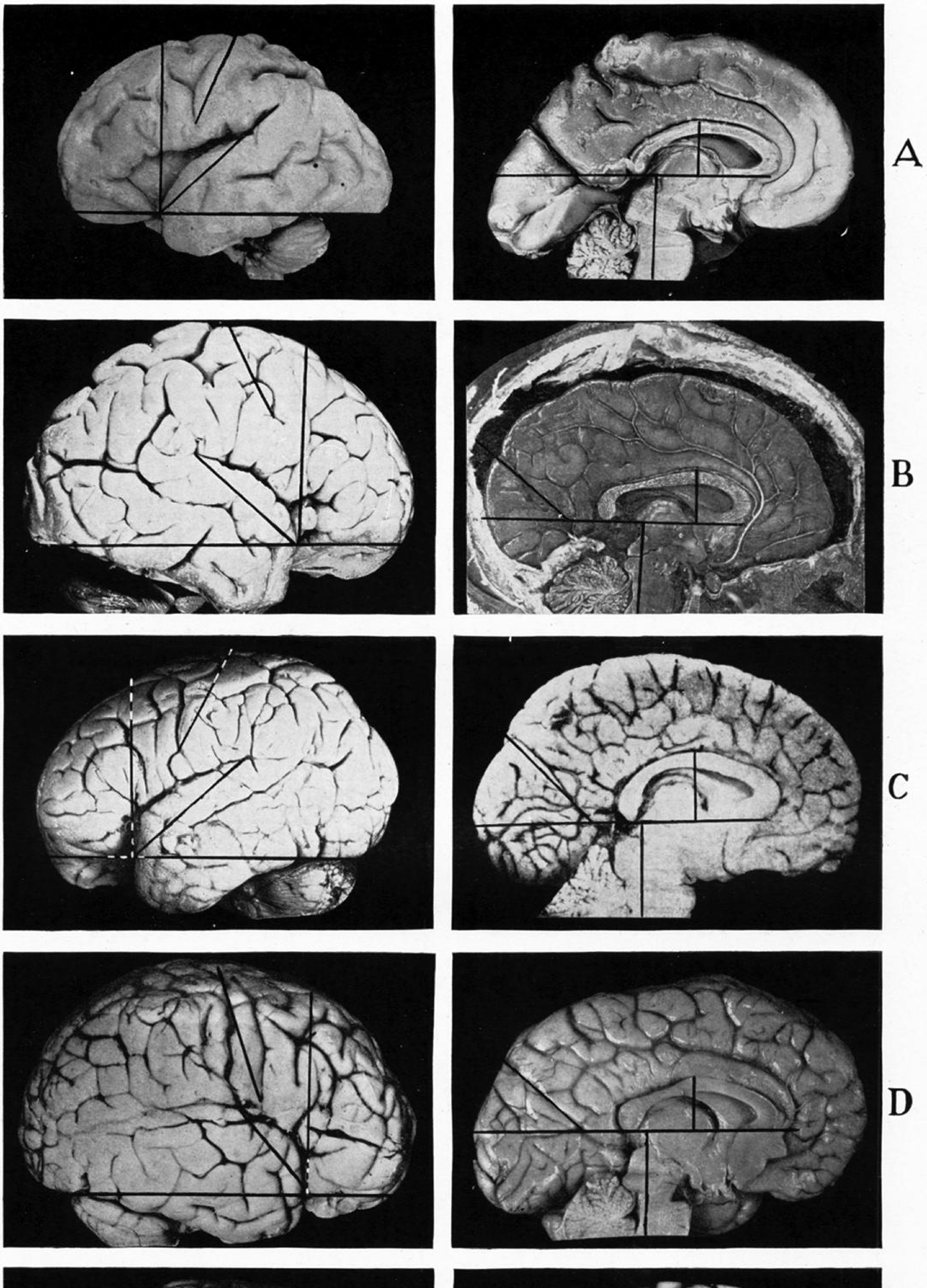

Plate 37.—A, the brain of a 7 months fœtus ; B and C, new-born brains ; D, the brain of a child of 1 month ; E, of 12 months.

In fig. B the lateral and mesial photographs are not of the same brain.

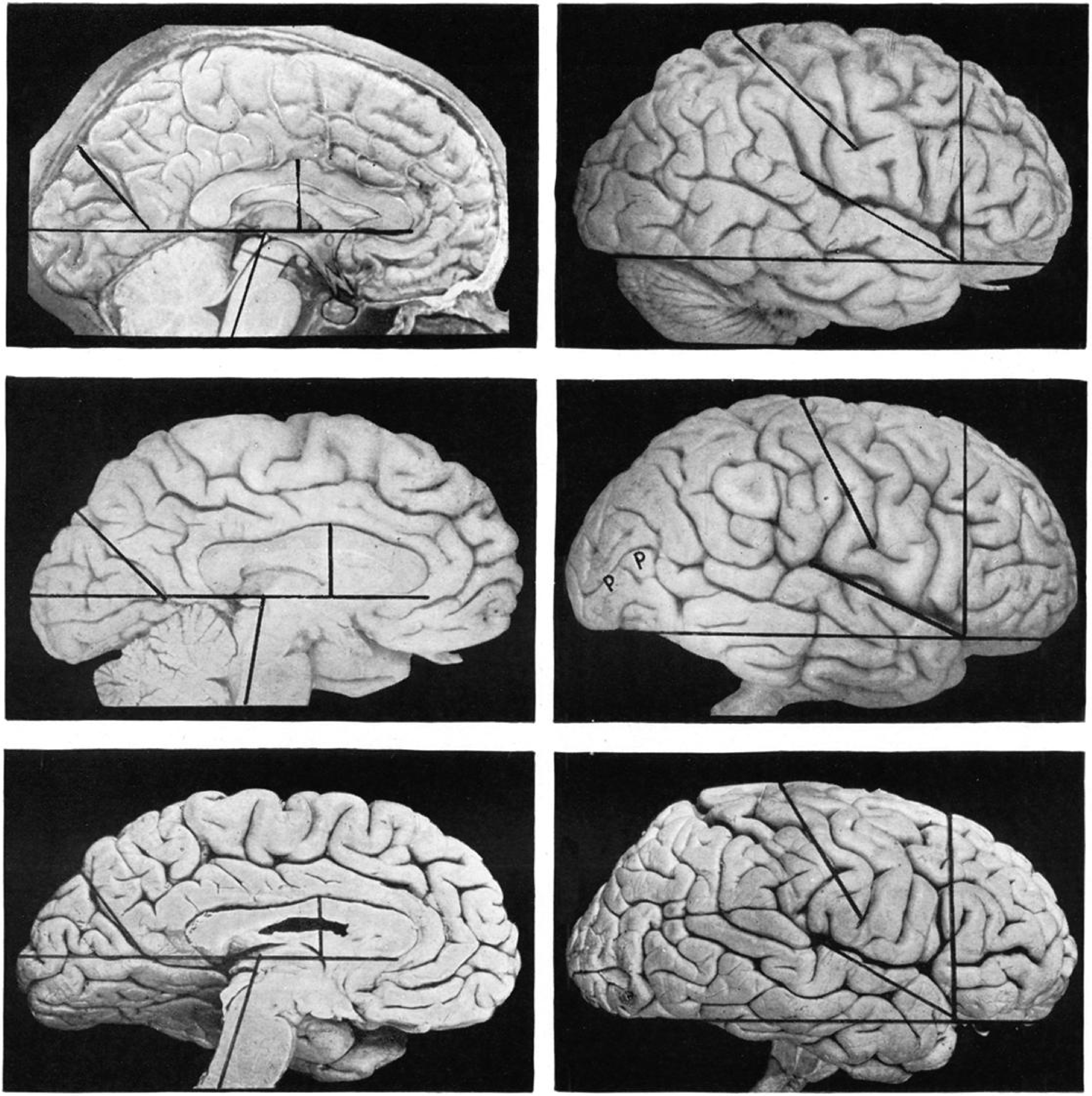

Plate 38.—Dolichocephalic Dutch brains. (The brain *in situ* is English.) P . . . P = prelunate sulcus.

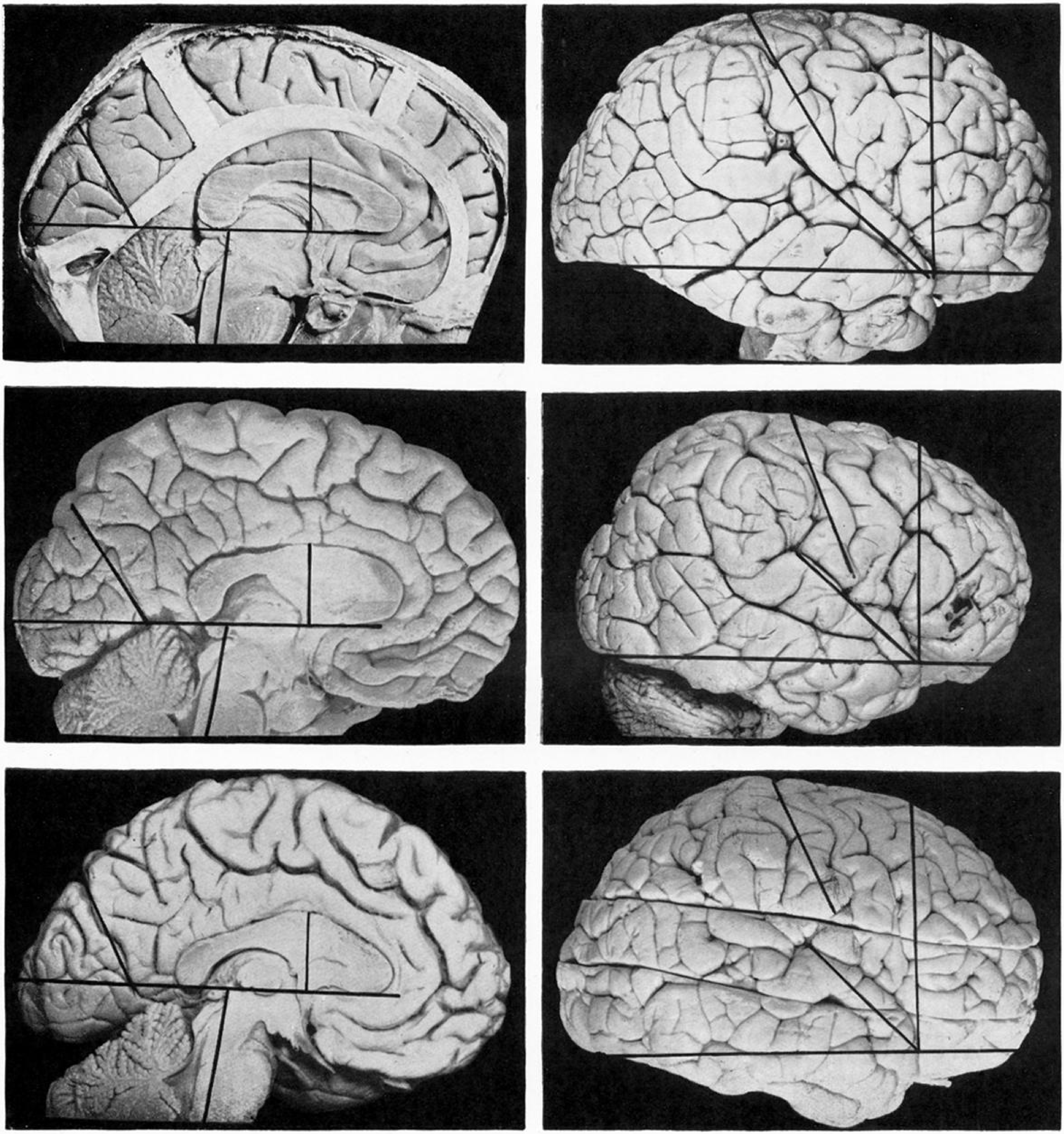

Plate 39.—Brachycephalic Dutch brains.

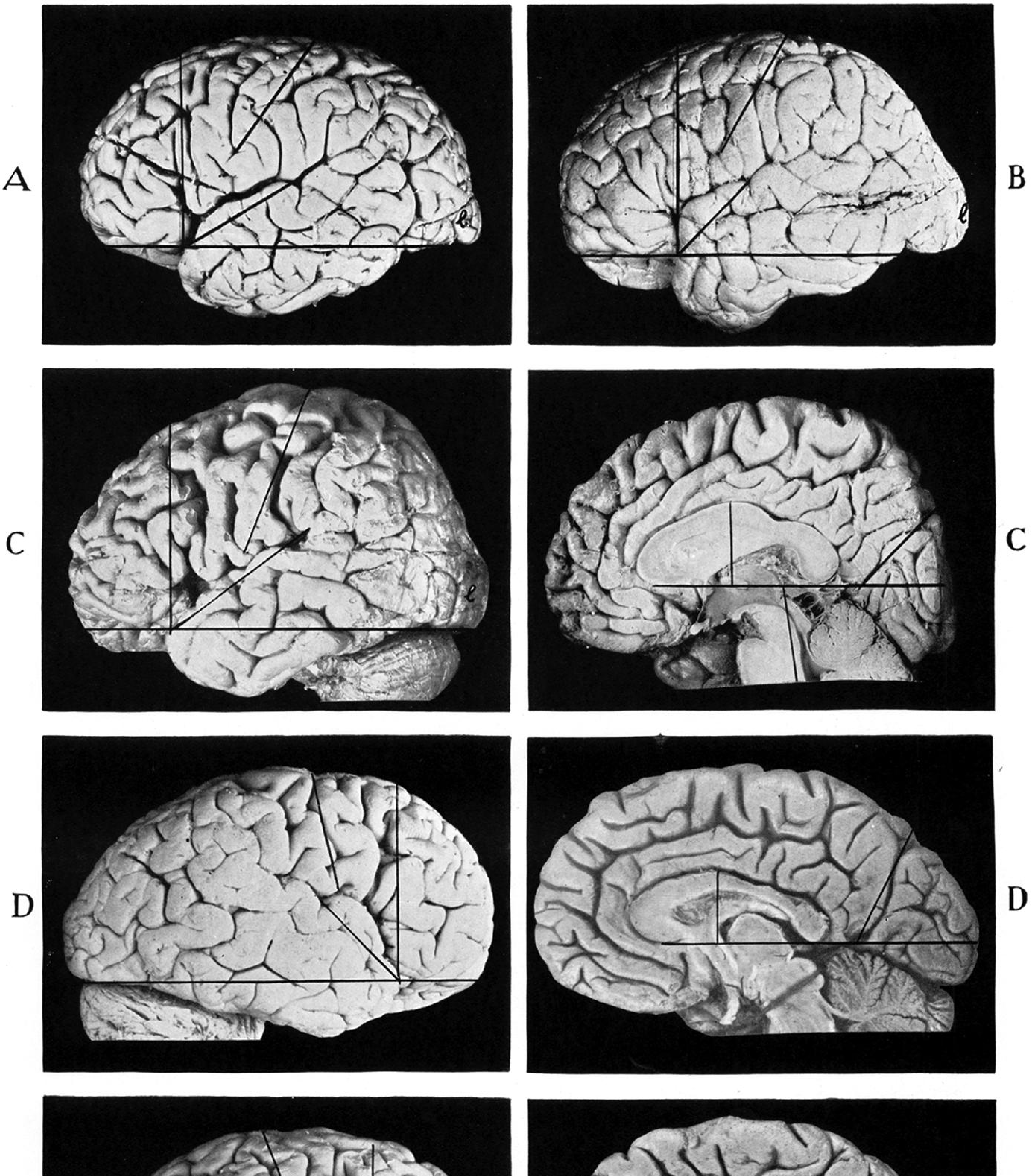

PLATE 40.—A, B, C, D, Armenian brains, and E, a Lebanese brain. The fissure in front of 1 is the lunate sulcus.

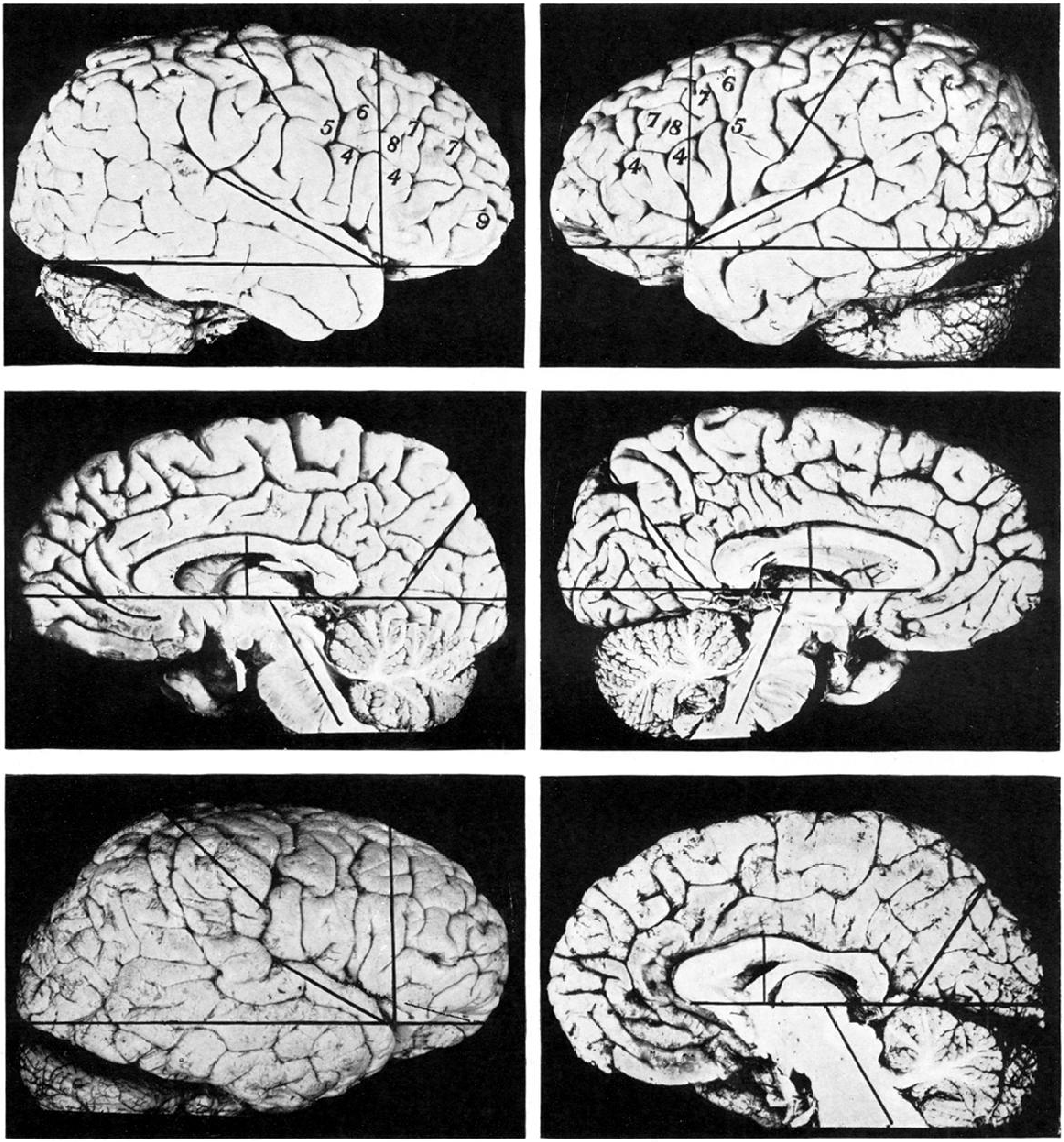

Plate 41.—Two brains of Egyptians (top : female brain, skull index 72·2 ; two lower figures : male brain, skull index 78).

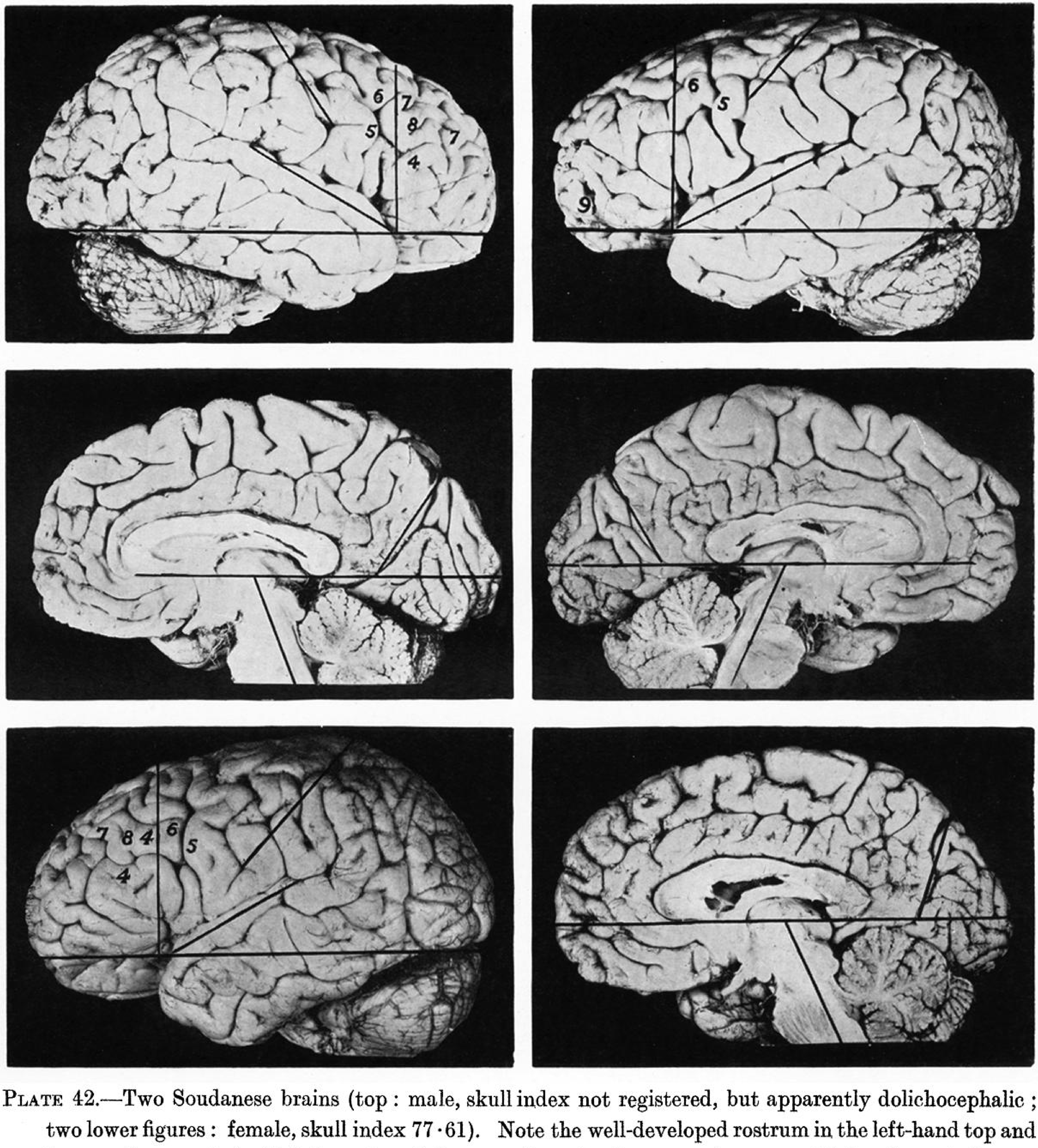

PLATE 42.—Two Soudanese brains (top : male, skull index not registered, but apparently dolichocephalic ; two lower figures : female, skull index 77·61). Note the well-developed rostrum in the left-hand top and bottom figure and the high insertion of the posterior calcarine, more frequent with brachycephalics.

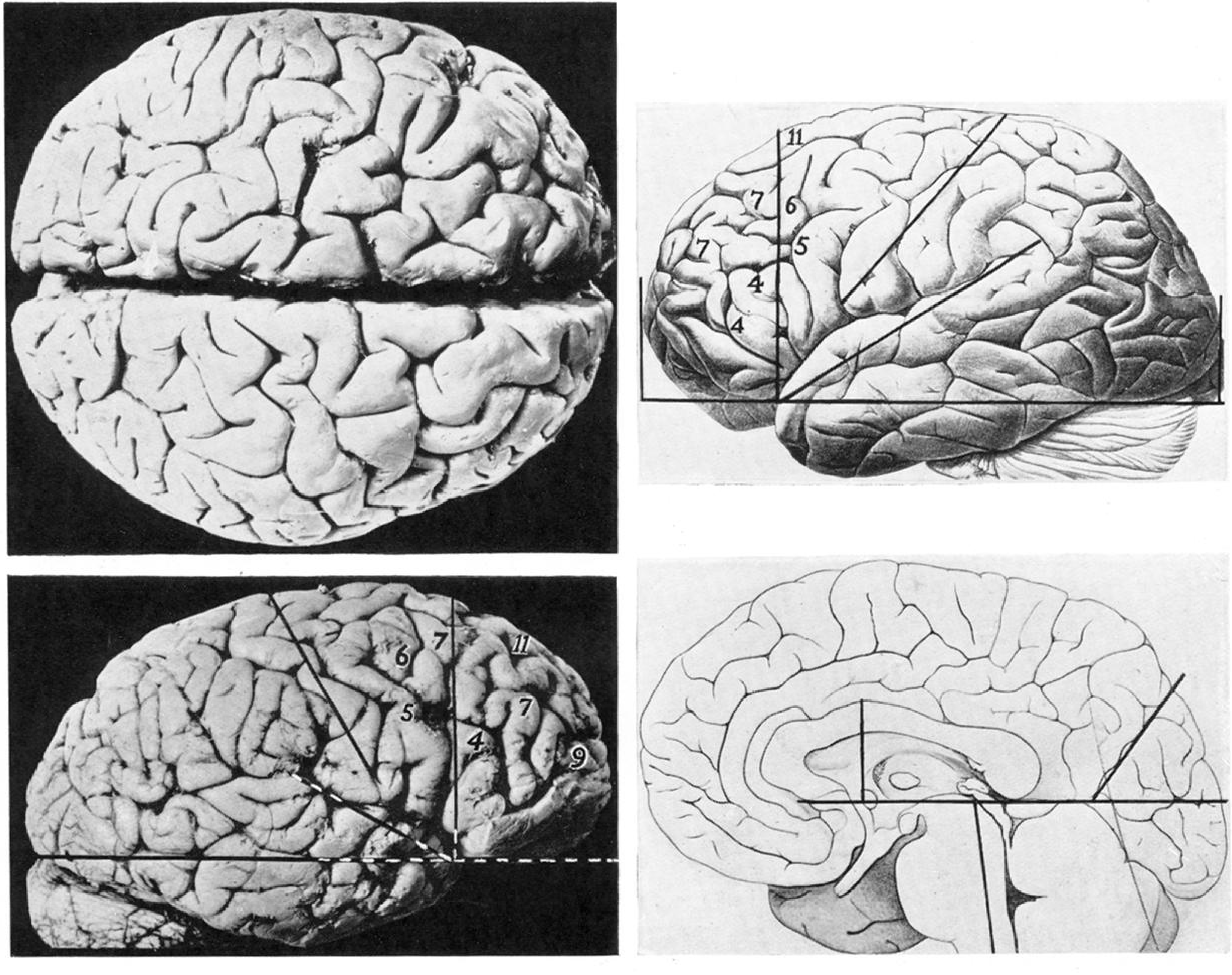

Plate 43—Brains of Northern Mongols (left by V. Stefko, right by G. Retzius).

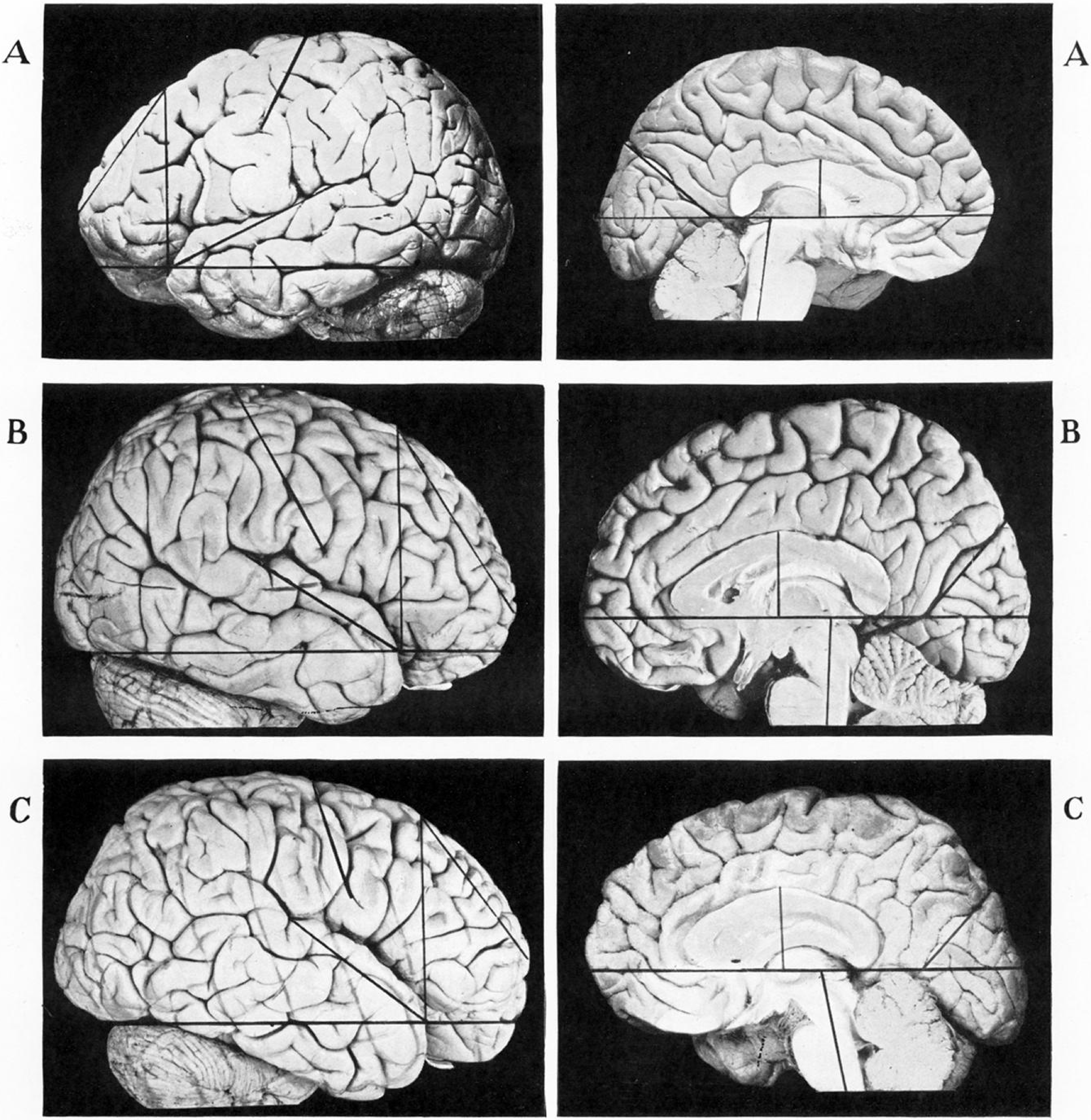

Plate 44.—Chinese brains. Brain index A = 83·7; B = 80·1; C = 77·7. The cephalic indices are about 1·5 to 2 lower.

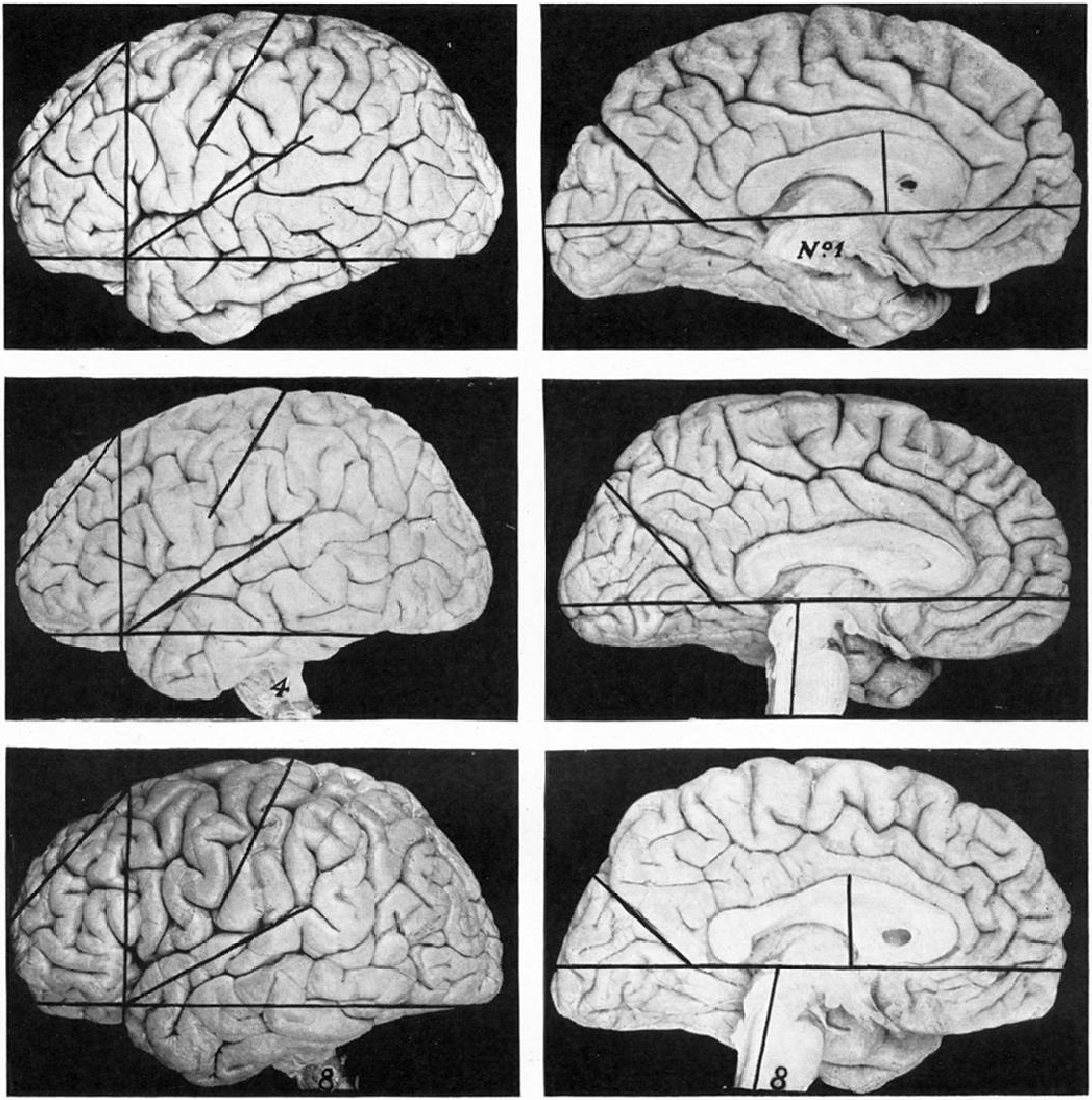

Plate 45.—Brains of Japanese from Sendai (North Japan).

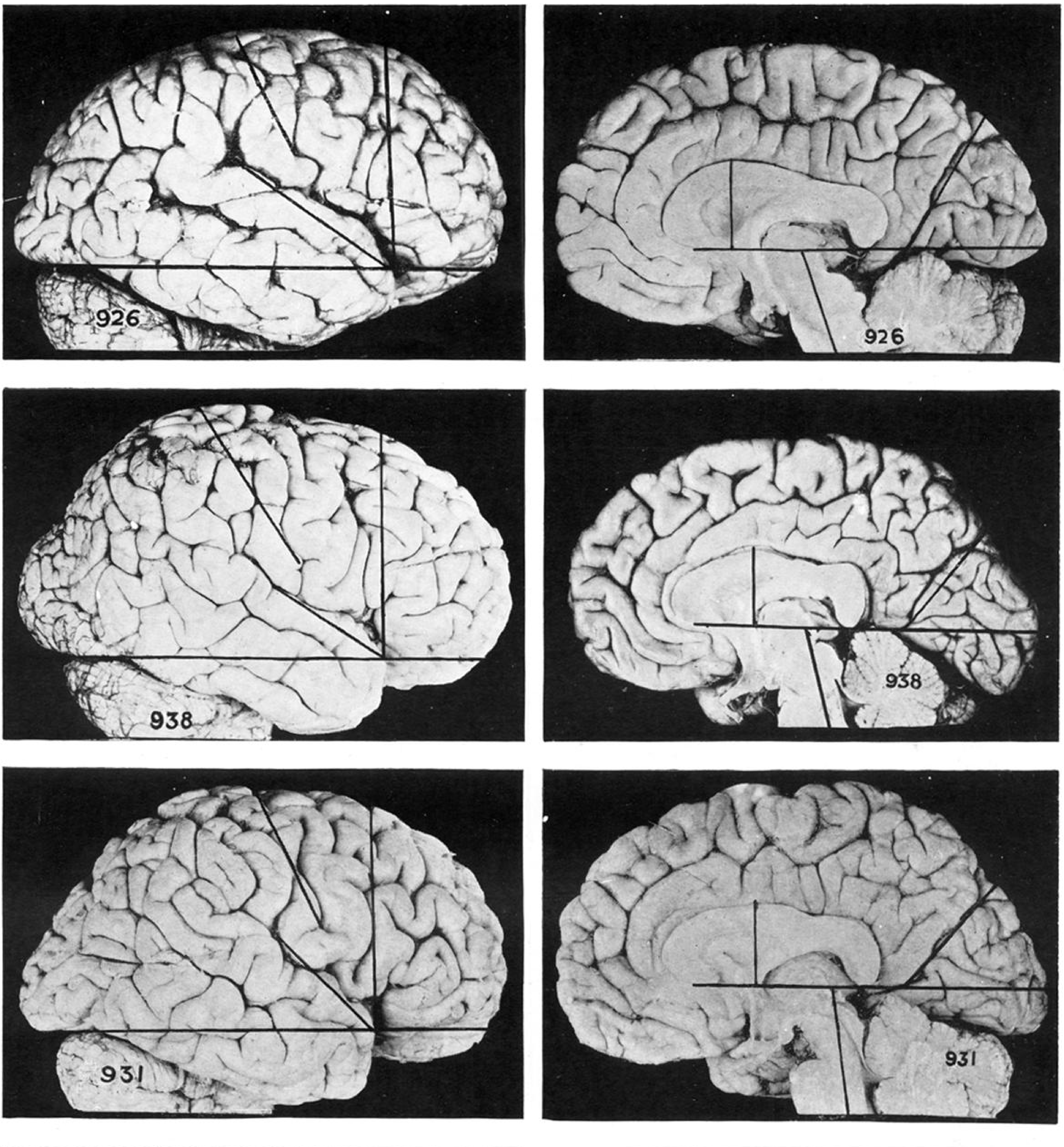

PLATE 46.—926 and 938, brain of a female and male Toba Batak, 931 and 934 brain of a female and male Karo Batak.

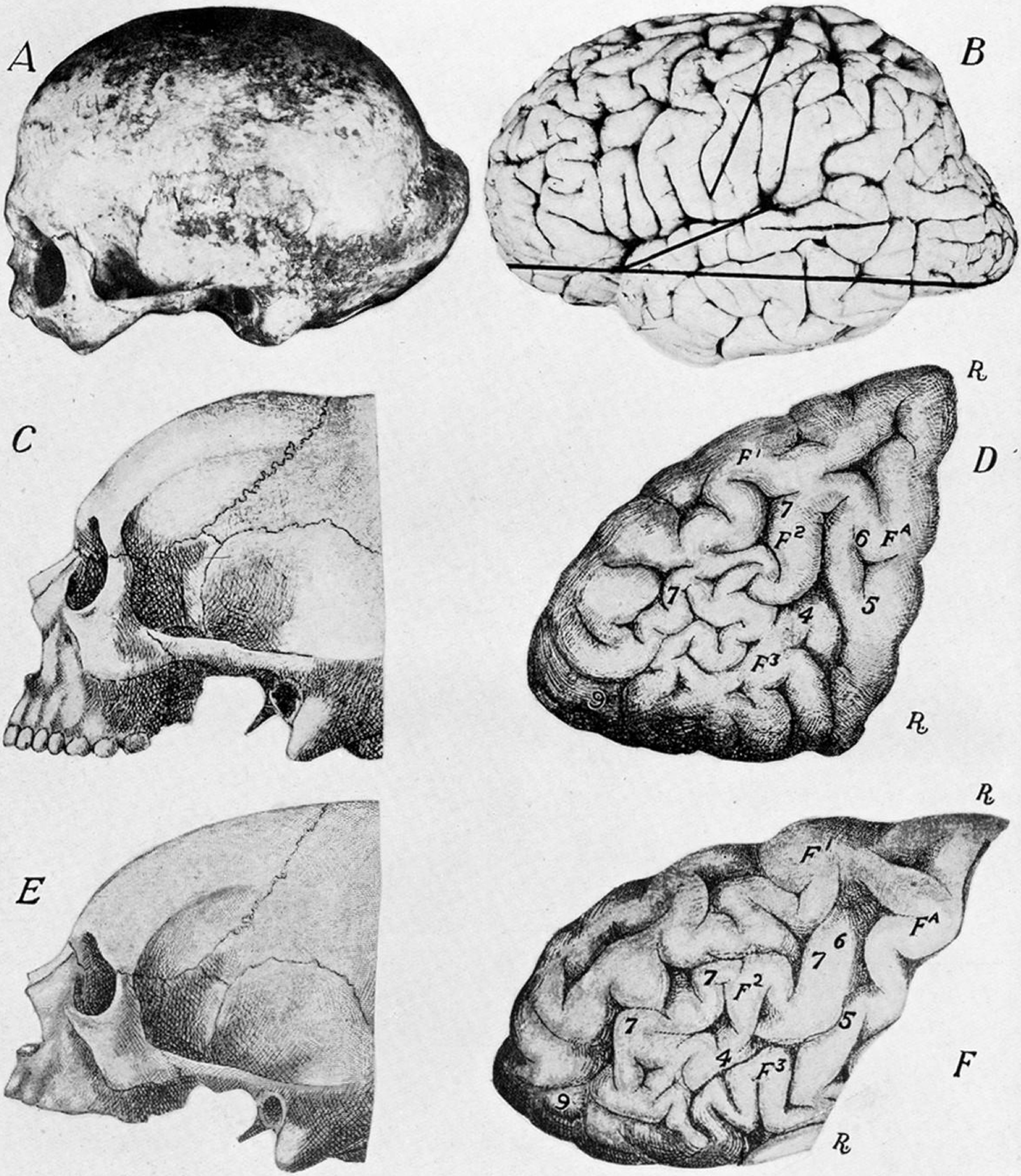

Plate 47.—A, Bathrocephalic Dutch skull; B, Bathrocephalic Batak brain; C and D, skull and brain of a deformed Toulousaine head (after Ambialet); E and F, skull and brain of a form artificially deformed frontally strongly sloping head (after Ambialet). R. . . R = Rolandic fissure. The deep dimple between 7 and 4 is my 8.

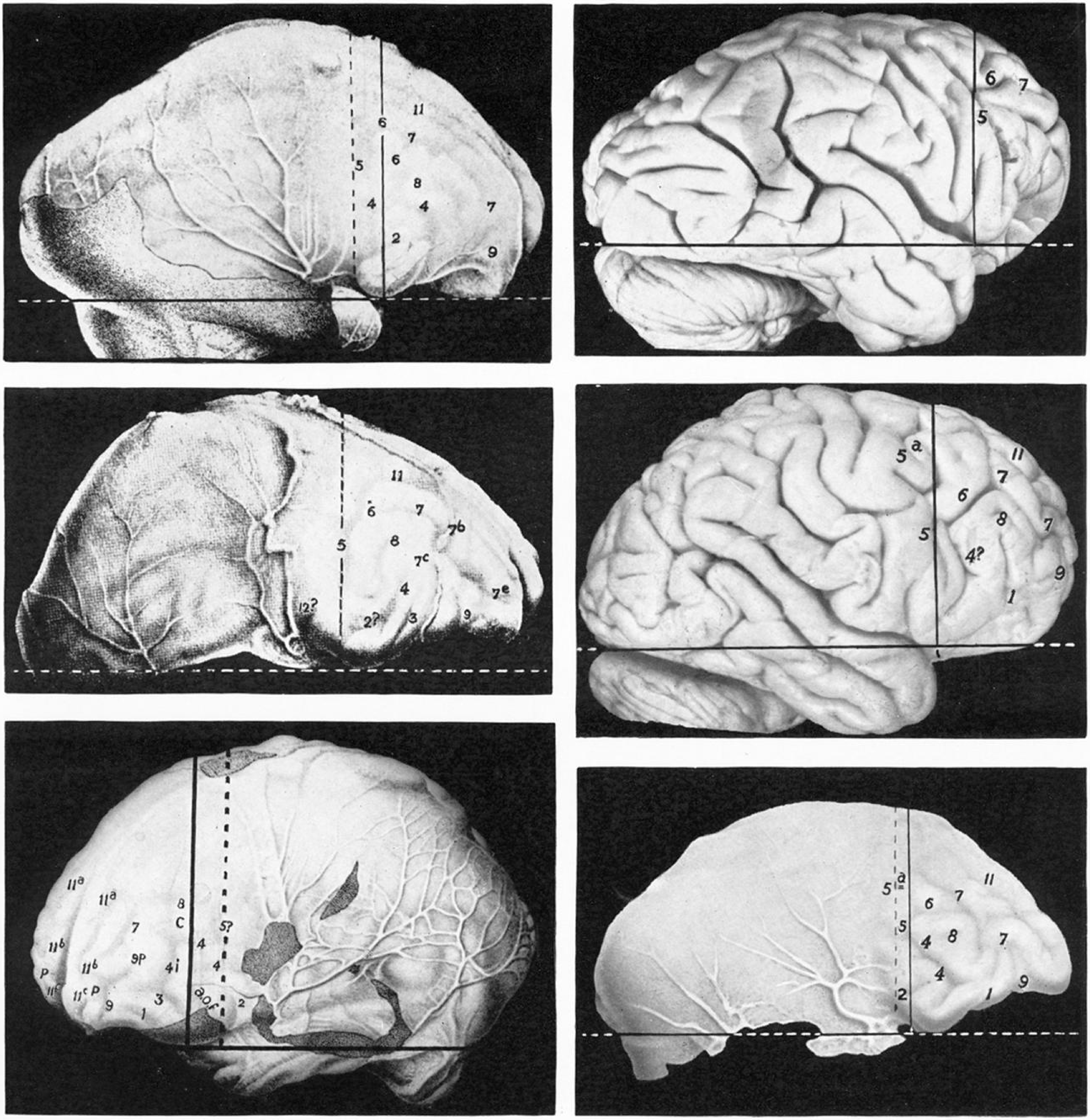

Plate 48.—Right from top, brain of an Orang-Utan and a Chimpanzee, left hemispheres reversed for easier comparison, with the right hemisphere of *Pithecanthropus erectus* (Dubois).

Left from the top, endocranial casts of the man of Rhodesia, Düsseldorf and Prdmost III.